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TWO JUVENILE GREAT WHITE SHARKS, *CARCHARODON CARCHARIAS* (LINNAEUS, 1758) (CHONDRICHTHYES; LAMNIDAE), CAUGHT IN THE NORTHEASTERN AEGEAN SEA

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ABSTRACT

Two juvenile female white sharks, Carcharodon carcharias (Linnaeus, 1758), were captured in coastal waters of the northeastern Aegean Sea. Both sharks were captured by means of commercial fishing gear. Total lengths of the specimen Nos. 1 and 2 were 180 and 300 cm. Two angler fish (Lophius spp.), one gar fish (Belone belone) and one hake (Merluccius merluccius) were found in the stomach contents of specimen No 1. Due to coastal occurrence of C. carcharias, regular monitoring and seasonal banning of coastal gill-netting and long-lining in the areas of the northeastern Aegean Sea, where white sharks are sighted, is necessary in order to minimize the impact of fishing on the species. Authors also discuss the current status of C. carcharias in Turkish waters, with respect to available data.

Key words: White shark, *Carcharodon carcharias*, coastal occurrence, Aegean Sea

DUE GIOVANI DI GRANDE SQUALO BIANCO, *CARCHARODON CARCHARIAS* (LINNAEUS, 1758) (CHONDRICHTHYES; LAMNIDAE), CATTURATI NELL'EGEO NORD-ORIENTALE

SINTESI

Due giovani femmine di squalo bianco, Carcharodon carcharias (Linnaeus, 1758), sono state catturate in acque costiere dell'Egeo nord-orientale. Entrambi gli esemplari sono stati pescati con attrezzature per pesca commerciale. Le lunghezze totali degli esemplari 1 e 2 erano rispettivamente di 180 e 300 cm. Due rane pescatrici (Lophius spp.), un'aguglia (Belone belone) ed un nasello (Merluccius merluccius) sono stati trovati nei contenuti stomacali dell'individuo No 1. Vista la presenza in acque costiere di C. carcharias, gli autori sottolineano la necessità di un monitoraggio regolare e divieti stagionali di pesca costiera, con reti a strascico e tramagli, nelle aree dell'Egeo nord-orientale dove gli squali bianchi vengono avvistati, al fine di minimizzare l'impatto della pesca su tale specie. Gli autori discutono anche lo stato attuale di C. carcharias in acque turche, tenendo conto dei dati disponibili.

Parole chiave: squalo bianco, *Carcharodon carcharias*, presenza costiera, mare Egeo

INTRODUCTION

Although early writings on the occurrence of the white shark, *Carcharodon carcharias* (Linnaeus, 1758), in Bosphoric and Marmaric waters date back into the last quarter of the 19th century (Fergusson, 1996; Kabasakal, 2003), and the first two decades of the 20th century (Ninni, 1923; Deveciyan, 1926; Ayaşlı, 1937), its presence in Bosphoric and Marmaric waters, as well as in Turkish seas has always been a point of controversy. Despite the historical records on *C. carcharias* from the Turkish Straits Systems – Dardanelles and Bosphorus straits, and the Sea of Marmara (Kabasakal, 2003), and its contemporary records from the Turkish Aegean Sea (Kabasakal & Kabasakal, 2004; Kabasakal, 2008; Kabasakal & Gedikoğlu, 2008), it's still questioned from time to time, whether the great white shark occurs in Turkish seas.

Following the recent captures of two newborn white sharks in the Edremit Bay (Kabasakal & Gedikoğlu, 2008), Ichthyological Research Society (I.R.S.) has intensified the field surveys among fishermen along the coast of the northeastern Aegean Sea in order to record any specimen of *C. carcharias* from the area. Similar efforts have been made in İstanbul city, where fishmongers purchased this so called "fearsome beast" for public display.

The present article deals with two juvenile great white sharks caught in the northeastern Aegean Sea. Authors also discuss the current status of *C. carcharias* in Turkish waters, with respect to available data.

MATERIAL AND METHODS

The present study is a part of an extensive area of research (KANIT Project – Türk Sularında Yaşayan Köpekbalıklarının Tesbiti Projesi (Identifying the Sharks of Turkish Waters); KANIT means "proof" in Turkish), which was initiated in 2000 by the IRS. Data on great white sharks has been collected from the following sources: (a) scientific literature; (b) daily newspapers, fishing magazines and other popular media, and as far as popular sources are concerned, the validity of the recordings has been confirmed by means of direct contact with the fishermen reported in the source; (c) visiting the fishing ports.

Both white sharks were captured in Turkish territorial waters (Fig. 1) by commercial fishing gear. The total lengths (TL) of the specimens were measured to the nearest cm. TL is the distance from the tip of the snout to the tip of the upper caudal lobe, where the caudal fin is placed in its natural position. Both specimens were photographed. Specimen No. 1 is now kept at Balıkesir University, Faculty of Arts and Sciences.



Fig. 1: Fishing localities of specimen Nos. 1 and 2 of the present study, and previous great white shark records from the northeastern Aegean Sea. Legend: 1 – specimen caught off Foça on 18th March 1991; 2 – specimen caught off Bozcaada in March 1996; 3 – specimen sighted south of Gökçeada in April 1998; 4 – specimen sighted in Saros Bay in May 1999; 5 and 6 – newborns caught in Edremit Bay, on 1st and 4th of July 2008, respectively; 7 – present specimen No. 1; 8 – present specimen No. 2.

Sl. 1: Lokaliteti, kjer sta bila ujeta obravnavana primerka št. 1 in 2, in predhodne zabeležbe pojavljanja velikega belega morskega volka v severovzhodnem Egejskem morju. Legenda: 1 – primerek, ujet v bližini kraja Foça 18. marca 1991; 2 – primerek, ujet pri otoku Bozcaada marca 1996; 3 – primerek, viden južno od otoka Gökçeada aprila 1998; 4 – primerek, viden v zalivu Saros maja 1999; 5 in 6 – novorojena primerka, ujeta v Edremitiskem zalivu 1. in 4. julija 2008; 7 – obravnavani primerek št. 1; 8 – obravnavani primerek št. 2.

Detailed observation of specimen No. 1 was carried out by the second author, Aylin Yarmaz (A.Y.); however, as specimen No. 1 is part of the on-going master thesis of A.Y., only fishing data (locality, fishing gear, etc.) of specimen No. 1 is given in the present paper, to prevent violating the originality of the dissertation. The third author, Sait Özgür Gedikoğlu (S.Ö.G.), an İstanbul based underwater videographer, could only measure the TL of specimen No. 2 and determine its sex. Unfortunately, the fishmonger did not allow S.Ö.G. to eviscerate the shark or take any samples from the teeth or tissues. Photographs of both specimens, and teeth from upper and lower jaws of specimen No. 1, are kept in the archives of I.R.S.

RESULTS

Specimen No. 1

On 21st February 2009, a female great white shark (Figs. 2, 3) was caught off Gökçeada (Fig. 1) by a bottom-trawler. After docking at Çanakkale harbour the captain of the trawler donated the specimen to Balıkesir University. Here the shark was measured and dissected. The total length of the shark was 180 cm and its total weight 47.5 kg. 26 teeth were counted in the upper jaw and 24 were in the lower jaw. Two angler fish (*Lophius* spp.), one gar fish (*Belone belone*) and one hake (*Merluccius merluccius*) were found in the stomach.

Specimen No. 2

On 15th April 2009, the second great white shark, a female of 300 cm TL and weighing 102 kg (Figs. 4, 5), was caught off Çanakkale coast (Fig. 1) by a commercial purse-seiner. As in many previous instances, after dock-

ing at Çanakkale harbour, specimen No. 2 was transported to İstanbul for public display at a fishmonger's. On 17th April, S.Ö.G. saw specimen No. 2 from the sidewalk and examined the shark. Unfortunately, the fishmonger did not allow to collect teeth or tissue samples. A few days later, specimen No. 2 was purchased by a collector for its jaws. All efforts of I.R.S. to access the jaws of specimen No. 2 failed.

DISCUSSION AND CONCLUSIONS

Female *C. carcharias* reach maturity at a total length between 450 and 500 cm (Casey & Prat Jr., 1985; Lipej *et al.*, 2004; Compagno *et al.*, 2005). The total lengths of specimen Nos. 1 and 2 were 180 and 300 cm, respectively; thus both great white sharks were juvenile specimens.

The first record of *C. carcharias* from the seas of Turkey dates back to February 1881, when 391 cm TL great white shark stranded off Beylerbeyi coast in the Bosphorus Strait (Fergusson, 1996). Kabasakal (2003) reviewed the historical records of *C. carcharias* from Turkish waters and concluded that almost all of them were from the Sea of Marmara. The great white shark had been a by-catch of tuna hand-liners in Bosphoric and Marmaric waters until the end of the 1970's (Kabasakal, 2003). Despite the historical accounts of *C. carcharias* from the Bosphorus Strait and the Sea of Marmara (Ninni, 1923; Deveciyan, 1926; Ayaşlı, 1937; Fergusson, 1996; Kabasakal, 2003, 2008), great white sharks from the Turkish coast of the Aegean Sea were accounted in specific studies only very recently (Kabasakal & Kabasakal, 2004; Kabasakal, 2008; Kabasakal & Gedikoğlu, 2008). Although Akşiray (1987), Mater & Meriç (1996) and Bilecenoğlu *et al.* (2002) reported *C. carcharias* from the Turkish coast of the Aegean Sea, there is no specific in-



Fig. 2: Specimen No. 1 (180 cm TL) caught off Gökçeada on 21st February 2009. (Photo: I.R.S. Archive)

Sl. 2: Primerek št. 1 (180 cm celotne dolžine), ujet pri otoku Gökçeada 21. 2. 2009. (Foto: Arhiv IRS)



Fig. 3: Teeth of specimen No. 1: scale = 1 cm. (Photo: I.R.S. Archive)

Sl. 3: Zobovje primerka št. 1; merilo = 1 cm. (Foto: Arhiv IRS)

formation available in these general ichthyological studies of where the examined specimens were caught or available for inspection.

The historical and contemporary occurrences of *C. carcharias* in the Mediterranean basin have been subjected to several investigations (Postel, 1958; Barrull, 1993–94; Fergusson, 1996, 2002; De Maddalena, 2000, 2002; Storai *et al.*, 2000, 2005; Barrull & Mate, 2001; Celona, 2002; Soldo & Jardas, 2002; Morey *et al.*, 2003; Megalofonou *et al.*, 2005; Saïdi *et al.*, 2005; Soldo & Dulčić, 2005; Cristo *et al.*, 2006). To date, 478 cases of great white sharks from the Mediterranean have been recorded (De Maddalena, 2006). According to Fergusson (1996), the Mediterranean distribution of *C. carcharias* is concentrated mainly in the western and central parts of the basin. Only 35 great white sharks, including the present specimens, have been recorded from the eastern Mediterranean, and the adjacent Aegean and Marmara Seas (Ben-Tuvia, 1971; Fergusson, 1996; Kabasakal, 2003; Kabasakal & Kabasakal, 2004; Kabasakal, 2008; Kabasakal & Gedikoğlu, 2008). The total number of great white sharks reported from the eastern Mediterranean and adjacent seas (35), constitutes 7.3 percent of the total number recorded by De Maddalena (2006).

The role played by sea surface temperatures (SSTs) in

affecting the distribution of great white sharks is demonstrated in the literature (Casey & Pratt, Jr., 1985; Nakaya, 1994; Fergusson, 1996; Barrull & Mate, 2001; Kabasakal, 2003; Morey *et al.*, 2003). Casey & Pratt, Jr. (1985) concluded that the 15°C isotherm is a rough indication of the seasonal great white shark distribution in the northern latitudes. *C. carcharias*, in the Mediterranean Sea tolerated SSTs ranging from 7.5°C to 25°C, but few cases were reported in waters with a temperature above 23°C (Fergusson, 1996). Three great white sharks, reported in Kabasakal & Kabasakal (2004) from the northeastern Aegean Sea, were captured or sighted between March and May, when SSTs ranged from 13°C to 18°C (Kocataş & Bilecik, 1992).

Specimen No. 2, reported in Kabasakal (2008) from the central Aegean Sea, was captured on 18th March 1991, when SST in the central Aegean Sea varied between 13°C and 14°C (Kocataş & Bilecik, 1992). Two newborn great white sharks, reported from Edremit Bay, were captured in late June and early July (SSTs 20–21.5°C). Specimen No. 1 of the present study was caught in February (SSTs 10–13°C) and specimen No. 2 was caught in April (SSTs 13–15°C). Although young great white sharks have a lower thermal tolerance for sea water temperature changes, an important factor limiting the



Fig. 4: Specimen No. 2 (300 cm TL) caught off Çanak-kale coast on 15th April 2009, and displayed at a fish-monger's in İstanbul. (Photo: I.R.S. Archive)

Sl. 4: Primerka št. 2 (300 cm celotne dolžine), ujet pri obali Çanak-kale 15. 4. 2009 in razstavljen v ribarnici v Istanbulu. (Foto: Arhiv IRS)



Fig. 5: A close-up view of the head and dentition of specimen No. 2. (Photo: I.R.S. Archive)

Sl. 5: Bližnji posnetek glave in zobovja primerka št. 2. (Foto: Arhiv IRS)

movement of juveniles (Casey & Pratt, Jr., 1985), eurythermal nature of the great white sharks suggests that the species can remain along the Turkish coast of the central and north Aegean Sea all year round. Weng *et al.* (2007) noted that, in the eastern Pacific, vertical excursions were deeper and cooler for 3-year-old great white sharks than young-of-the-year specimens.

According to Klimley (1985), pups remain inshore and as they grow larger, they live both inshore and near offshore islands. Fishing data of 8 great white sharks from the Turkish coast of the north Aegean Sea revealed that all specimens were caught or seen in coastal and insular waters (Kabasakal & Kabasakal, 2004; Kabasakal, 2008; Kabasakal & Gedikoğlu, 2008). The proximity of offshore islands to Edremit Bay, which is clearly seen on the map in figure 1, creates an advantageous locality for newborn and growing great white sharks for moving between coastal and offshore waters.

The central Mediterranean Sea has long been considered as a nursery site for great white sharks because of the previous and recent captures of pregnant females with developing and near-term embryos, as well as free-swimming juveniles, particularly in the Gulf of Gabés (Fergusson, 1996; Saïdi *et al.*, 2005). On the other hand, the possibility of a breeding ground for *C. carcharias* in the eastern Mediterranean basin has always been debatable. In addition to the recent captures of two newborn great white sharks off the Altınoluk coast (Kabasakal & Gedikoğlu, 2008), capture of the present juvenile great white sharks off Gökçeada and Çanakkale coasts provides extra evidence supporting the presumption of a breeding ground in the northeastern Aegean Sea, extending from Edremit Bay to the north of Gökçeada (Fig. 1).

The stomach examination of 54 young great white sharks caught in the northwest Atlantic showed a diet comprised primarily of demersal fish (Casey & Pratt, Jr., 1985). According to Weng *et al.* (2007), benthic foraging is important for the juvenile great white sharks. Benthic prey, mainly fish, was also observed in the stomach contents of small great white sharks (< 300 cm TL) from California waters (Tricas & McCosker, 1984). Benthic prey (*Lophius* spp. and *M. merluccius*) was found in the stomach contents of specimen No. 1 of the present study. A sparid fish (*Sparidae* spp.) was found in the stomach contents of the newborn great white shark (142 cm TL) from Edremit Bay (Kabasakal & Gedikoğlu, 2008). Piscivorous foraging habits of young great white sharks are an important factor increasing the possibility of incidental captures of juveniles in coastal fishing gear. The occurrence of *C. carcharias* in different regions of the Mediterranean basin is associated with the presence of tuna stocks (Boero & Carli, 1979; De Maddalena, 2000; Vacchi *et al.*, 2002; Morey *et al.*, 2003; Cristo *et al.*, 2006). The introduction of intensive tuna fishing and the following drastic decline of tuna (*Thunnus thynnus*)

stocks resulted in a clear decline, even a total disappearance of great white sharks in many parts of the Mediterranean and the adjacent seas, e.g., eastern Adriatic waters (Soldo & Jardas, 2002), Marmaric waters (Kabasakal, 2003), Balearic waters (Morey *et al.*, 2003; Fromentin & Powers, 2005). The intensive fishing of major prey of *C. carcharias* is a major anthropogenic impact on the decline of great white sharks in the Mediterranean.

Today more data is available on the great white sharks from Turkish waters; however, new data brings new questions. What is the rate of encounters with fishing nets and the associated mortality? What are the larger-scale movement patterns and what is the extent of their movements along the Turkish coast? Do the juvenile great white sharks exhibit diurnal onshore/offshore movements? When and where are the juveniles feeding? Is the great white shark a resident or a vagrant species in the northeastern Aegean Sea? In contrast to previous suggestions that the great white shark is a questionable or extinct species in Turkish waters, available data revealed that *C. carcharias* is still occurring off the Turkish coast. Regarding the entire coastal line of Turkey, the regularity of this occurrence remains unclear; however, regular occurrence of newborns and young great white sharks in Turkish coastal waters of the north Aegean Sea is well-documented in Kabasakal & Gedikoğlu (2008) and in the present study. Several popular diving spots are also located within the boundaries of this possible nursing ground. Thousands of swimmers, as well as skin and scuba divers visit the area between late spring and early autumn. Seasonal co-existence of man and the great white shark is another major concern jeopardizing the survival of *C. carcharias*. To the best of our (authors) knowledge, no shark attack by great white sharks or other large sharks in the northeastern Aegean Sea has been recorded to date. However, increasing occurrence of great white sharks in the area may cause an aggressive interaction between man and shark, not only in the form of a shark attack, but also creating public fear and an increase in the killing of great white sharks.

Fricke *et al.* (2007) considered the great white shark a highly endangered species in Turkey, as well as a very sensitive species to human activity. For IUCN in the Mediterranean the species is vulnerable (Serena, 2005), *C. carcharias* is listed on Appendix II of the Bern Convention, as well as CITES Appendix III, since 28th May 2003 (Compagno *et al.*, 2005; Serena, 2005; Fricke *et al.*, 2007). The great white sharks are now protected in some parts of the world (Compagno *et al.*, 1997); however, due to their migratory habits, a worldwide cooperation is necessary for the survival of the species. Currently, there is no measurement for the protection of *C. carcharias* set in the Fisheries Act of Turkey. The great white sharks and other large sharks caught mainly by commercial fishing boats operating in Turkish waters are

often sold to a small but lucrative market, primarily for their jaws. Although the great white shark can descend to a depth of 1300 m (Serena, 2005), it is primarily a coastal and offshore inhabitant of continental and insular shelves (Compagno, 1984). Due to the coastal occurrence of *C. carcharias*, regular monitoring and seasonal banning of coastal gill-netting and long-lining in the areas, where white sharks are sighted in the northeastern

Aegean Sea, is necessary in order to minimize the impacts of fishing on the species.

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DVA MLADOSTNA VELIKA BELA MORSKA VOLKA, *CARCHARODON CARCHARIAS* (LINNAEUS, 1758) (CHONDRICHTHYES; LAMNIDAE), UJETA V SEVERNOVZHODNEM EGEJSKEM MORJU

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POVZETEK

Dve mladostni samici velikega belega morskega volka, *Carcharodon carcharias* (Linnaeus, 1758), sta bili ujeti v obalnih vodah severnovzhodnega Egejskega morja, obe z opremo za gospodarski ribolov. Primerek št. 1 je v celotno dolžino meril 180 cm, primerek št. 2 pa 300 cm. V vsebini želodca primerka št. 1 so našli dve morski spaki (*Lophius spp.*), iglico (*Belone belone*) in osliča (*Merluccius merluccius*). Zaradi pojavljanja *C. carcharias* v obalnih vodah bi bil na območju severovzhodnega Egejskega morja, kjer so beli morski volki videni, nujno potreben reden monitoring in sezonska prepoved obalnega ribolova z zabodno mrežo in vlečnimi mrežami, da se zmanjša vpliv ribolovnih dejavnosti na to vrsto. Avtorji razpravljajo tudi o trenutnem statusu *C. carcharias* v turških vodah.

Ključne besede: beli morski volk, *Carcharodon carcharias*, pojavljanje v obalnih vodah, Egejsko morje

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NEW BIOLOGICAL DATA ON THORNBAC RAY, *RAJA CLAVATA* (CHONDRICHTHYES: RAJIDAE), OFF THE LANGUEDOCIAN COAST (SOUTHERN FRANCE, NORTHERN MEDITERRANEAN)

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ABSTRACT

*Investigations conducted off the Languedocian coast (southern France, the northern Mediterranean) allowed the authors of this paper to capture 252 specimens of the thornback ray *Raja clavata* (Linnaeus, 1758) and to present information on hepatosomatic index (HSI) and gonadosomatic index in both males and females which significantly increased with the size of specimens. A positive relation was observed between the mass of oviducal glands and size (as disc width). Oviducosomatic index (OSI), was only calculated in females. HSI, GSI and OSI reached the maximum values in adult specimens. These indexes did not show significant changes throughout the year, suggesting that reproductive activity of *R. clavata* occurred permanently.*

Key words: Chondrichthyes, *Raja clavata*, liver, gonads, oviducal glands, Languedocian coast, Mediterranean

NUOVI DATI BIOLOGICI SU RAZZA CHIODATA, *RAJA CLAVATA* (CHONDRICHTHYES: RAJIDAE), AL LARGO DELLA COSTA DI LANGUEDOC (FRANCIA MERIDIONALE, MEDITERRANEO SETTENTRIONALE)

SINTESI

*Ricerche condotte al largo della costa di Languedoc (Francia meridionale, Mediterraneo settentrionale) hanno permesso agli autori di catturare 252 individui di razza chiodata *Raja clavata* (Linnaeus, 1758) e di presentare informazioni inerenti l'indice epatosomatico (HSI) e l'indice gonadosomatico in maschi e femmine. I valori degli indici aumentavano significativamente con l'aumentare della grandezza degli individui. Gli autori hanno osservato una correlazione positiva fra la massa delle ghiandole dell'ovidotto e la grandezza (ossia larghezza del disco corporeo). L'indice oviducosomatico (OSI) è stato calcolato solo per le femmine. Gli indici HSI, GSI e OSI hanno raggiunto i valori massimi negli individui adulti. Tali indici non hanno evidenziato differenze significative nell'arco dell'anno, il che suggerisce che l'attività riproduttiva di *R. clavata* è permanente.*

Parole chiave: Chondrichthyes, *Raja clavata*, fegato, gonadi, ghiandole dell'ovidotto, costa di Languedoc, Mediterraneo

INTRODUCTION

According to Chavelot *et al.* (2006), prior to the 1950s, the thornback ray *Raja clavata* Linnaeus, 1758 was common and widely distributed in the seas of northwest Europe. Since then, it has decreased in abundance and geographic range due to over-fishing and its *K*-selected biological characteristics (*sensu* McAuley *et al.*, 2007), such as in other elasmobranch species, for instance growth rate, late maturity and low fecundity, that make *R. clavata* susceptible to exploitation as victims of by-catch in northern European marine regions (Hunter *et al.*, 2005; Whittamore & McCarthy, 2005). Similar patterns were observed in specimens from other Mediterranean areas such as the coast of Languedoc (Capapé *et al.*, 2006, 2007); the rare landings of specimens collected in the area in a 16-year period showed a decline of captures. However, Garofalo *et al.* (2003) noted an increasing abundance trend of *Raja clavata* on the southwest side of the Sicilian shelf, due to the fact that fishing pressure in the area considerably decreased in the last ten years.

Additionally, the thornback ray is not abundant off the Mediterranean coast of Turkey (H. Kabasakal, *pers. comm.*), however, the species is abundant and targeted by the fishermen deploying bottom fishing gear off the Black Coast of Turkey (mainly along the western shoreline), as well as in the Sea of Marmara (H. Kabasakal, *pers. comm.*; Torku Koç *et al.*, 2004; Saglam & Bascinar, 2008). The thornback ray *R. clavata* was formerly known as relatively abundant throughout the Tunisian coast, (Capapé, 1976). At present, this skate is rather commonly landed even if it is locally considered as a by-catch species (Mnasri, 2008).

The reproductive biology of *R. clavata* was previously studied from specimens caught off the British coasts (Steven, 1936; Chevolut *et al.*, 2007), the Atlantic coast (Du Buit, 1968) and the Mediterranean coast of France (Capapé *et al.*, 2007), the Adriatic Sea (Zupanic, 1961; Jardas, 1973) and the Tunisian coast (Capapé, 1976, 1979). Investigations conducted during a 16-year period off the coast of Languedoc (Mediterranean shore of France) allowed us to collect specimens of *R. clavata* and data on some traits of its reproductive biology, such as size at sexual maturity, reproductive cycle and fecundity (Capapé *et al.*, 2007). Therefore, in this paper, we provide additional observations on thornback rays by analyzing variations of gonadosomatic and hepatosomatic indexes in both sexes, and oviducosomatic index only in females, in order to try to detect seasonal variations in the gonadal production. Our results are compared and contrasted with those carried out in thornback rays from other regions, such as off the Tunisian coast (Capapé, 1979).

MATERIAL AND METHODS

A total of 252 specimens were studied, 114 males and 138 females. Samples of *Raja clavata* were collected by gill-netters and trawlers at depths up to 80 m, on sandy and muddy bottoms between November 1988 and December 2008, between 43° and 43°30' N, and between 3°40' and 4°15' E. They were generally landed at the harbours of Palavas-Les-Flots and Sète. Moreover, research surveys were conducted in the same areas on board of the oceanographic trawler 'Georges Petit', in November 1988 and 1990 and May 1992 and 1993 (see Capapé *et al.*, 2007).

Disc width (DW) of the specimens was measured to the nearest millimetre following Clark (1926) and mass (TM) was measured to the nearest gram, liver, gonads and oviducal glands masses to the nearest decigram. Clasper length was measured from the forward rim of the pelvic girdle to the tip of the clasper following Colenot (1969). Three stages of male maturity were considered relative to the degree of calcification of claspers and the morphology of the genital duct, following Capapé *et al.* (2007). They were juvenile, sub-adult and adult. Similar stages were also considered in females from the condition of ovaries, the morphology of the reproductive tract and the mass of oviducal glands following Callard *et al.* (2005) and Capapé *et al.* (2007). Hepatosomatic index (HSI), gonadosomatic index (GSI) were calculated in both males and females, as

$$\text{HSI} = (\text{LM}/\text{TM}) \times 100; \text{LM} = \text{liver mass}$$

$$\text{GSI} = (\text{GM}/\text{TM}) \times 100; \text{GM} = \text{gonad mass}$$

while the oviducosomatic index (OSI) was calculated only in females, as

$$\text{OSI} = (\text{OM}/\text{TM}) \times 100; \text{OM} = \text{oviducal glands mass}$$

Variations in GSI, HSI and OSI related to size were considered in all categories of specimens in both sexes, while monthly variations were only considered in adult males and females.

Tests for significance ($p < 0.05$) were performed by using ANOVA, with special regard to variations in HSI, GSI and OSI related to size, while monthly comparisons were performed using non-parametric H-test of Kruskal-Wallis. The linear regression was expressed in decimal logarithmic coordinates. Correlations were assessed by least-squares regression.

RESULTS

Juvenile males ranged in size between 110 and 370 mm DW and weighed between 31 and 985 g; they were mostly caught in March and between May and August. Juvenile females ranged between 110 and 440 mm DW and weighed between 440 and 1645 g; captures mainly occurred in November (Tab. 1).

Sub-adult males were between 350 and 440 mm DW and weighed between 840 and 2598 g. The specimens were caught throughout the year. Sub-adult females were 410 and 540 mm DW and weighed between 3300 and 4950 g; they were captured in May, April, August and December.

The smallest adult male was 420 mm DW and weighed 2130 g, while the largest specimen was 510 mm DW and weighed 4500 g; some specimens were collected every month. The smallest adult female was 540 mm DW and weighed 4950 g; the largest was 690 mm DW and weighed 5980 g; captures occurred throughout the year. The mass of both oviducal glands (OG Mass) was weighed in the three categories of females. The relationship between DW and OG Mass was: $\log \text{OG Mass} = 4.678 \log \text{DW} - 11.513$; $r = 0.884$ (Fig. 1).

Values of HSI recorded in male *Raja clavata* ranged between 1.74 and 6.76 (mean = 4.22 ± 1.16), while in females they ranged between 1.44 and 6.90 (mean = 3.51 ± 0.79). Considering the whole sample (see Fig. 2A) these values were significantly higher in males than in females ($F = 82.13$, $df = 1$, $p < 0.001$). Values of male HSI showed significant changes according to stages *i.e.*, juvenile, sub-adult and adult (Fig. 2B). HSI values in juvenile males ranged between 1.74 and 6.42 (mean = 3.56 ± 1.04), they ranged between 2.20 and 6.42 (mean = 4.47 ± 1.02) in sub-adults and between 2.69 and 6.76 (mean = 5.05 ± 0.83) in adults. As in males, values of female HSI showed significant changes according to age stages (Fig. 2C). HSI values in juvenile females ranged between 1.76 and 4.10 (mean = 3.16 ± 0.59), they ranged between 2.29 and 6.02 (mean = 3.88 ± 1.2) in sub-adults and between 2.29 and 6.90 (mean = 3.69 ± 0.43) in adults. Values of female HSI, (Fig. 6) showed significant changes between juveniles and sub-adults ($df = 2$, $p < 0.001$), by contrast these changes were not significant between sub-adults and adults ($df = 2$, $p = 0.69$).

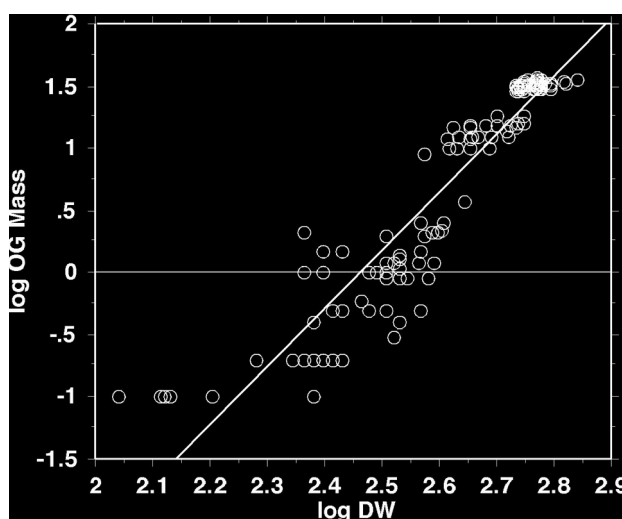


Fig. 1: Relationship between Oviducal Gland Mass (OG Mass) and Disc Width (DW) expressed in logarithmic co-ordinates for female *Raja clavata*.

Sl. 1: Razmerje med maso jajcevodnih žlez (OG) in širino telesne plošče (DW) pri samici vrste *Raja clavata*, izraženo v logaritmičnih koordinatah.

Concomitantly, values of male GSI ranged between 0.15 and 0.93 (mean = 0.48 ± 0.15), while in females they ranged between 0.1 and 6.00 (mean = 1.55 ± 0.46). However, in the whole sample (see Fig. 3A) these values were significantly higher in females than in males ($F = 80.29$, $df = 1$, $p < 0.001$). GSI both regularly and significantly increased between juveniles and sub-adults ($df = 2$, $p < 0.001$), and between sub-adults and adults ($df = 2$, $p = 0.024$). Similarly, values of male GSI showed significant changes according to the three stages *i.e.*, juvenile, sub-adult and adult (Fig. 3B). GSI values in juveniles ranged between 0.15 and 0.74 (mean = 0.38 ± 0.12), they ranged between 0.32 and 0.86 (mean = 0.51 ± 0.12)

Tab. 1: Monthly collection of the observed *Raja clavata* captured off the coast of Languedoc.

Tab. 1: Mesečna zbirka opazovanih raž trnjevk *Raja clavata*, ujetih v obalnih vodah Languedoca.

Sex	Category	Months												
		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Males	Juveniles	-	4	8	-	10	12	9	8	4	-	-	2	57
	Sub-adults	3	3	2	3	3	3	3	1	2	1	1	-	25
	Adults	2	1	2	4	3	2	2	2	3	3	2	6	32
	Total	5	8	12	7	16	17	14	11	9	4	3	8	114
Females	Juveniles	4	7	3	3	3	3	2	8	3	4	13	4	57
	Sub-adults	4	2	2	1	8	2	2	-	2	1	1	1	26
	Adults	2	4	3	1	5	6	5	2	7	4	10	6	55
	Total	10	13	8	5	16	11	9	10	12	9	24	11	138
Grand total		15	21	20	12	32	28	23	21	21	13	27	19	252

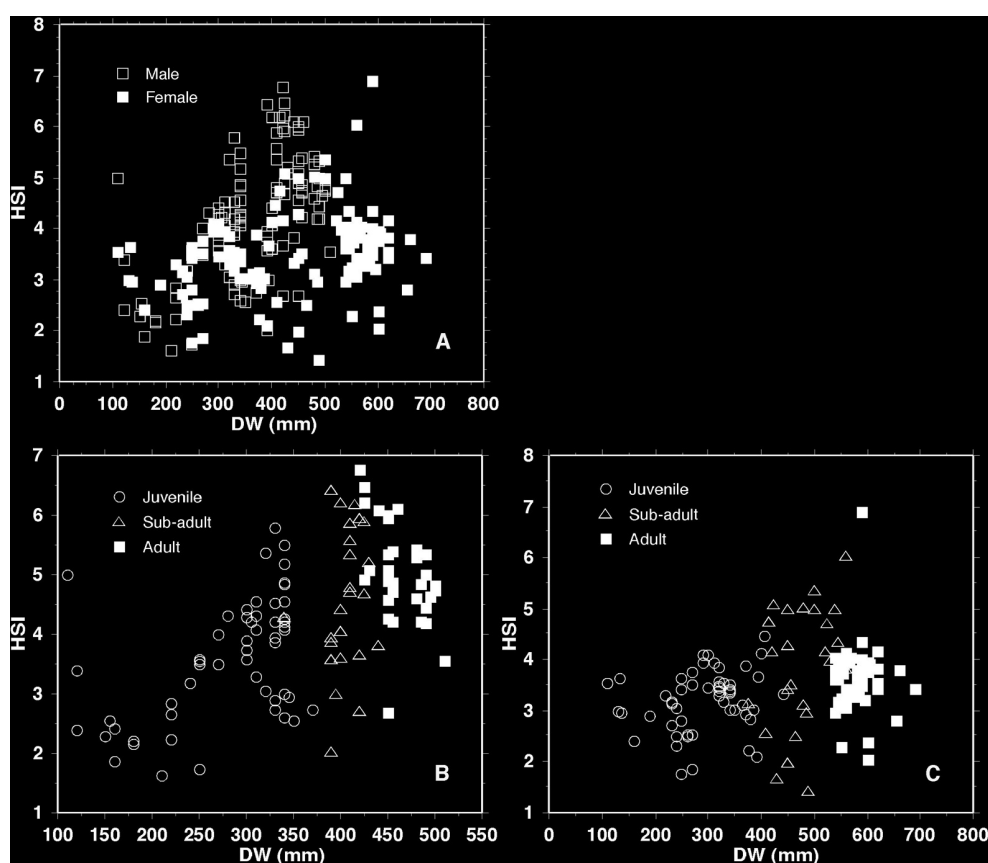


Fig. 2: (A) Variations in hepatosomatic index (HSI) vs. Disc Width (DW) in male and female *R. clavata*. (B) Variations in hepatosomatic index (HSI) vs. Disc Width (DW) in juvenile, sub-adult and adult male *R. clavata*. (C) Variations in hepatosomatic index (HSI) vs. Disc Width (DW) in juvenile, sub-adult and adult female *R. clavata*.

Sl. 2: (A) Variacije hepatosomatskega indeksa (HSI) vs. širina telesne plošče (DW) pri samcih in samicah vrste *R. clavata*. (B) Variacije hepatosomatskega indeksa (HSI) vs. širina telesne plošče pri mladostnih, subadultnih in odraslih samcih vrste *R. clavata*. (C) Variacije hepatosomatskega indeksa (HSI) vs. širina telesne plošče pri mladostnih, subadultnih in odraslih samicah vrste *R. clavata*.

in sub-adults and between 0.40 and 0.93 (mean = 0.56 ± 0.13) in adults. GSI both regularly and significantly increased between juveniles and sub-adults ($df = 2$, $p < 0.001$), and between sub-adults and adults ($df = 2$, $p = 0.024$). Values of female GSI ranged between 0.10 and 1.50 (mean = 0.45 ± 0.42) in juveniles, they ranged between 0.30 and 1.97 (mean = 0.60 ± 0.25) in sub-adults and between 1.14 and 5.35 (mean = 2.09 ± 1.50) in adults (Fig. 3C). GSI both regularly and significantly increased between juveniles and sub-adults ($df = 2$, $p < 0.001$), and between sub-adults and adults ($df = 2$, $p = 0.024$). Values of OSI, only recorded in females, (Fig. 4), showed significant changes between juveniles and sub-adults and between sub-adults and adults ($df = 1$, $p < 0.001$). These values ranged between 0.10 and 0.40 (mean = 0.20 ± 0.05), between 0.30 and 0.40 (mean = 0.38 ± 0.08) and between 0.50 and 0.99 (mean = 0.64 ± 0.07), in juveniles, sub-adults and adults, respectively.

The monthly mean values of adult male HSI plotted in Figure 5A did not show significant variations throughout the year ($H = 7.12$, $df = 11$, $p = 0.78$). As in males, the monthly mean values of adult female HSI plotted in Figure 5B did not show significant variations throughout the year, ($H = 11.24$, $df = 11$, $p = 0.42$). Similar patterns were observed in monthly mean values of adult male GSI (Fig. 6A), although it exhibited low values in April and December ($H = 11.4$, $df = 11$, $p = 0.41$), while monthly mean values of adult female GSI (Fig. 6B) exhibited low values in March and October, and a high value in December. However, these monthly differences were not significant ($H = 17.03$, $df = 11$, $p = 0.23$). Additionally, monthly mean values of OSI in adult females (Fig. 7) did not show significant changes ($H = 14.28$, $df = 11$, $p = 0.19$).

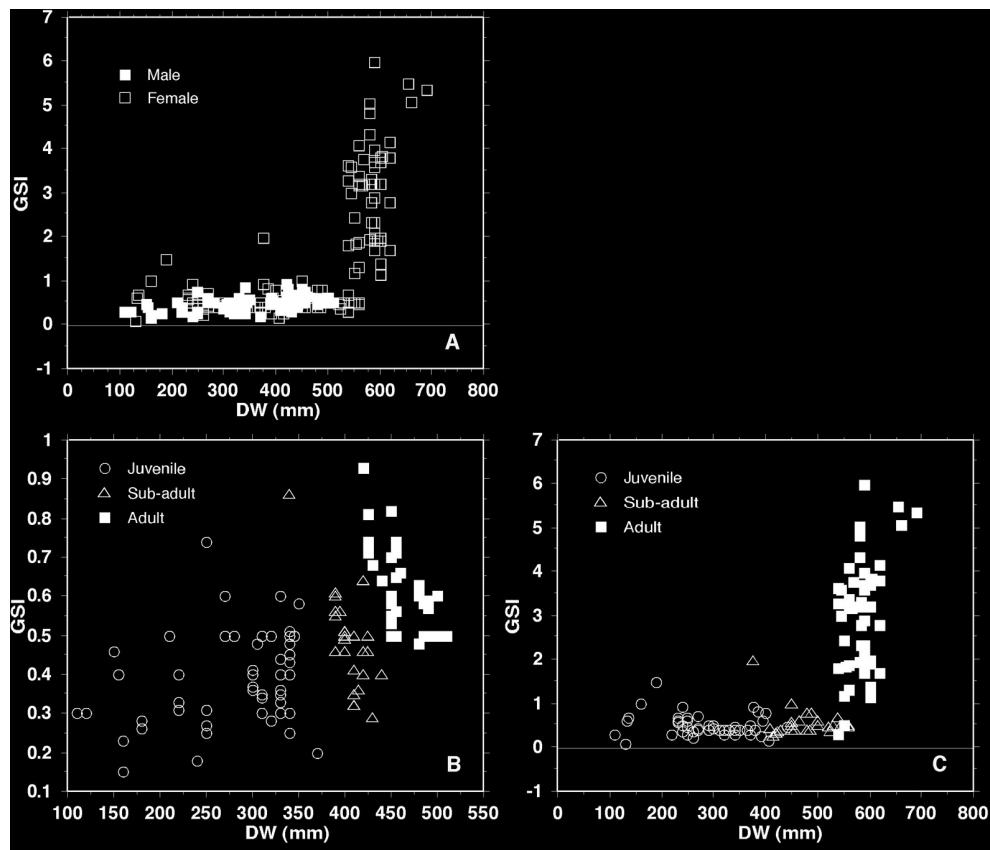


Fig. 3: (A) Variations in gonosomatic index (GSI) vs. Disc Width (DW) in male and female *R. clavata*. (B) Variations in gonosomatic index (GSI) vs. Disc Width (DW) in juvenile, sub-adult and adult female *R. clavata*. (C) Variations in gonosomatic index (GSI) vs. Disc Width (DW) in juvenile, sub-adult and adult female *R. clavata*.

Sl. 3: (A) Variacije gonosomatskega indeksa (GSI) vs. širina telesne plošče (DW) pri samcih in samicah vrste *R. clavata*. (B) Variacije gonosomatskega indeksa (GSI) vs. širina telesne plošče pri mladostnih, subadultnih in odraslih samcih vrste *R. clavata*. (C) Variacije gonosomatskega indeksa (GSI) vs. širina telesne plošče pri mladostnih, subadultnih in odraslih samicah vrste *R. clavata*.

DISCUSSION

Previous observations carried out on thornback rays from the Languedocian coast showed positive relationships between disc width and liver mass in both males and females (Capapé *et al.*, 2007). These observations were corroborated by regular increasing of HSI values in three categories of specimens, juveniles, sub-adults and adults, even if in females significant differences in HSI values between sub-adults and adults did not appear. All these observations confirm the liver role in buoyancy in agreement with previous reports (Bones & Roberts, 1969; Baldrige Jr., 1970, 1972; Capapé *et al.*, 2008a, b), but also its role in reproduction. A large liver plays an important role in gonadal products, especially in females, such as the production of yolk in both viviparous and oviparous species (García-Garrido *et al.*, 1990; Magrabaña *et al.*, 2002; Capapé *et al.*, 2008a). Liver stores nutrients which are transferred and used for fabrication of

gonadal products. This phenomenon is more important in females than in males, due to the fact that vitellogenesis occurs throughout the year. It could explain why HSI was significantly higher in males than in females, especially in adults. HSI values varied between 3.5 and 6.0 in female *R. clavata* from both the Languedocian and Tunisian coast (Capapé, 1979). Close HSI values between 1.55 and 6.30 were reported by Oddone *et al.* (2008) for female of the eye-spot skate *Atlantoraja cyclophora* (Regan, 1903) from off southeastern Brazil. Higher values, 6.5 and 10, were reported in the oviparous smallspotted catshark *Scyliorhinus canicula* (Linnaeus, 1758) from the coast of Languedoc (Capapé *et al.*, 2008a) and the Tunisian coast (Capapé, 1978). However, they are lower than those reported in viviparous species from the Languedocian coast, such as a HSI value of 14 calculated in the eagle ray *Myliobatis aquila* (Linnaeus, 1758) according to Capapé *et al.* (2008b), and especially in the angular rough shark *Oxynotus centrina* (Linnaeus, 1758), where

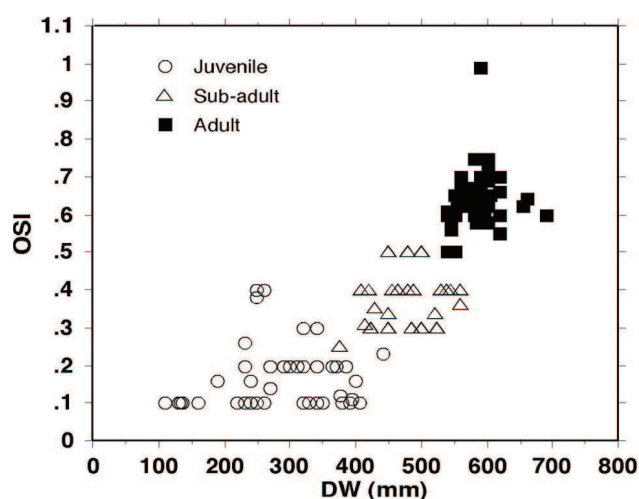


Fig. 4: Variations in oviducosomatic index (OSI) vs. Disc Width (DW) in juvenile, sub-adult and adult female *R. clavata*.

Sl. 4: Variacije ovidukosomatskega indeksa (OSI) vs. širina telesne plošče (DW) pri mladostnih, subadultnih in odraslih samicah vrste *R. clavata*.

Capapé *et al.* (1999) noted that they varied between 23.0 and 42.2, and Dragicevic *et al.* (2009) reported a HSI of 35.5 in a female caught in the eastern Adriatic Sea.

GSI was significantly higher in female *R. clavata* than in the male ones, due to the fact that female adults produce large, heavy and numerous yolky oocytes and vitellogenesis. Consequently, the reproductive activity occurs throughout the year (Capapé *et al.*, 2007), in agreement with the regular and significant increasing of GSI during the different stages of maturation in specimens of both sexes. Additionally, monthly changes of GSI were not significant in either males or females, corroborating the permanence of reproductive activity in all adult specimens throughout the year (see Capapé *et al.*, 2007). Similar patterns were reported for *R. clavata* from the Tunisian coast (Capapé, 1976, 1979), and other oviparous species such as skates (Oddone & Velasco, 2006; Oddone *et al.*, 2007, 2008) or sharks (Capapé, 1977, 1978; Capapé *et al.*, 2008a).

The positive relationship between disc width and mass of oviducal glands (see Fig. 1) showed that the development of oviducal glands considerably and signifi-

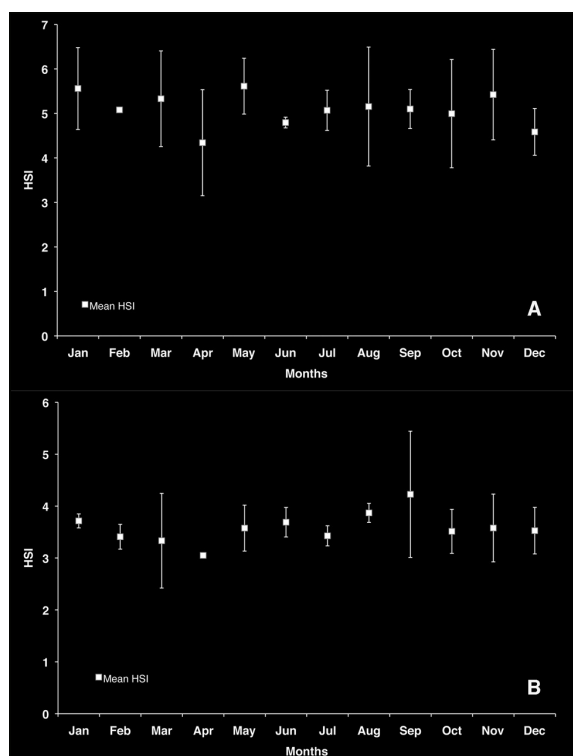


Fig. 5: (A) Monthly variations in hepatosomatic index (HSI) in male *R. clavata*. (B) Monthly variations in hepatosomatic index (HSI) in female *R. clavata*.

Sl. 5: (A) Mesečne variacije hepatosomatskega indeksa (HSI) pri samcih vrste *R. clavata*. (B) Mesečne variacije hepatosomatskega indeksa (HSI) pri samicah vrste *R. clavata*.

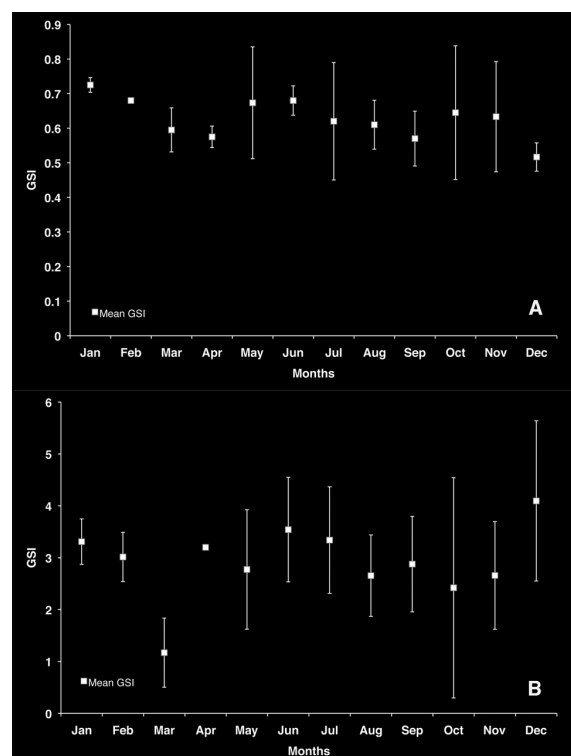


Fig. 6: (A) Monthly variations in gonosomatic index (GSI) in male *R. clavata*. (B) Monthly variations in gonosomatic index (GSI) in female *R. clavata*.

Sl. 6: (A) Mesečne variacije gonomatskega indeksa (GSI) pri samcih vrste *R. clavata*. (B) Mesečne variacije gonosomatskega indeksa (GSI) pri samicah vrste *R. clavata*.

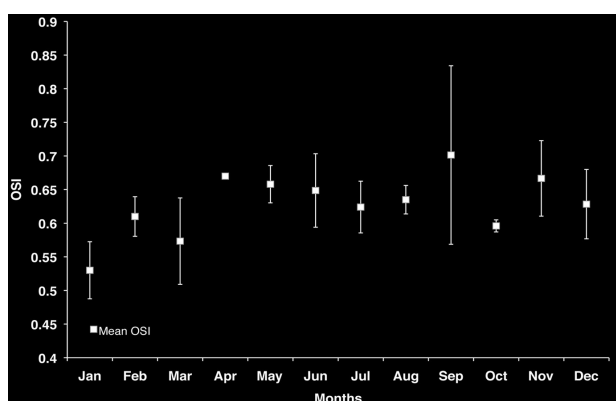


Fig. 7: Monthly variations in oviducosomatic index (OSI) in female *R. clavata*.

Sl. 7: Mesečne variacije ovidukosomatskega indeksa (OSI) pri samicah vrste *R. clavata*.

cantly increased in juveniles, sub-adults and adults. Capapé *et al.* (2007) reported that this development could be used as a good parameter to assess size at sexual maturity in oviparous species. The oviducal glands are well developed in adult oviparous species. Additionally, no significant changes throughout the year suggest that the reproductive activity is permanent, activity of oviducal glands and vitellogenesis being linked in all oviparous elasmobranch species.

NOVI BIOLOŠKI PODATKI O RAŽI TRNJEVKI, *RAJA CLAVATA* (CHONDRICHTHYES: RAJIDAE), IZ OBALNIH VOD LANGUEDOCA (JUŽNA FRANCIJA, SEVERNO SREDOZEMLJE)

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POVZETEK

V okviru raziskave, izvedene ob languedoški obali (južna Francija, severno Sredozemlje), so avtorji pričujočega članka proučili 252 primerkov raže trnjevke *Raja clavata* (Linnaeus, 1758) in sedaj predstavljajo podatke o hepatosomatskem indeksu (HSI) in gonadosomatskem indeksu pri samcih in samicah. Ta sta z velikostjo primerkov znatno porasla. Ugotovljena je bila tudi pozitivna korelacija med maso jajcevodnih žlez in velikostjo (oz. širino telesne plošče). Ovidukosomatski indeks (OSI) je bil merjen samo za samice. HSI, GSI in OSI so dosegli najvišje vrednosti pri odraslih primerkih. Indeksi se med letom niso spreminjali, kar kaže na stalno razmnoževalno aktivnost vrste *R. clavata*.

Ključne besede: Chondrichthyes, *Raja clavata*, jetra, spolne žleze, jajcevodne žleze, languedoška obala, Sredozemlje

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CETACEAN RECORDS AND ENCOUNTER RATES IN THE NORTHERN ADRIATIC SEA DURING THE YEARS 1988–2007

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ABSTRACT

We report a total of 156 cetacean sightings made in the northern Adriatic Sea between 1988 and 2007. Confirmed identifications ($n = 97$) involved exclusively common bottlenose dolphins *Tursiops truncatus*. Encounter rates for this species, obtained between 2001 and 2006 during visual cetacean surveys, ranged between 0.42 and 1.67 groups per 100 km of navigation, with no significant differences among years if a consistent methodology was used. Information provided by this study contributes to setting environmental baselines and it can inform the design of surveys aimed to obtain absolute estimates of cetacean abundance in this part of the Adriatic.

Key words: cetaceans, Adriatic Sea, common bottlenose dolphin, *Tursiops truncatus*

OSSERVAZIONI DI CETACEI E FREQUENZE DI AVVISTAMENTO IN ADRIATICO SETTENTRIONALE NEL PERIODO 1988–2007

SINTESI

Riportiamo un totale di 156 avvistamenti di cetacei in Adriatico settentrionale, dal 1988 al 2007. Le identificazioni confermate ($n = 97$) hanno riguardato esclusivamente il tursiope *Tursiops truncatus*. Le frequenze di avvistamento per questa specie, ottenute nel corso di survey visivi sui cetacei svolti tra il 2001 e il 2006, oscillavano tra 0,42 e 1,67 gruppi per 100 km di navigazione, senza differenze significative tra un anno e l'altro quando la metodologia era omogenea. Le informazioni qui fornite contribuiscono a stabilire dei punti di riferimento sullo stato dell'ambiente e possono essere utili nella progettazione di survey finalizzati all'ottenimento di stime di abbondanza assoluta dei cetacei in questa parte dell'Adriatico.

Parole chiave: cetacei, Mare Adriatico, tursiope, *Tursiops truncatus*

INTRODUCTION

Monitoring cetacean populations is crucial for understanding the changes occurring over time, including the extent of geographic occurrence and shifts in species composition. Of the two cetacean species regularly occurring in the northern Adriatic Sea until the 1960s – the common bottlenose dolphin *Tursiops truncatus* (hereafter "bottlenose dolphin") and the short-beaked common dolphin *Delphinus delphis* – the latter has declined dramatically due to anthropogenic impacts and it has become increasingly rare in this and other parts of the Mediterranean Sea (Bearzi *et al.*, 2003, 2004).

This study reports a total of 156 cetacean sightings recorded in the northern Adriatic Sea between 1988 and 2007. In addition, encounter rates of bottlenose dolphins were obtained through visual surveys conducted between 2001 and 2006. While a comprehensive and dedicated effort would be needed to assess cetacean abundance and gain insight into population status and trends, datasets such as the one presented here are relevant to understanding shifts in species composition and patterns of distribution. Encounter rates have relative value because results depend largely on methodology. However, they may provide preliminary insight in areas with poor quantitative information. Further, they can assist in the design of dedicated aerial or ship surveys by indicating the amount of minimum effort needed to obtain a given number of cetacean sightings (appropriate sample size being a pre-requisite of insightful analyses). The rationale behind the information presented here is therefore twofold: 1) contribute to setting environmental baselines for the understanding of changes occurring over time (e.g. decades or centuries; Sáenz-Arroyo *et al.*, 2005), as requested *inter alia* by the EC Marine Strategy Framework Directive (2008/56/EC of 17 June 2008), and 2) present information that can inform the design of surveys (e.g. Buckland *et al.*, 1993) intended to obtain absolute estimates of cetacean abundance in this part of the Adriatic.

MATERIAL AND METHODS

Cetacean sighting records were collected opportunistically between 1988 and 2007 by observers including experienced cetacean researchers, biologists carrying out other kind of research, Customs Authority officers, pleasure boaters and sailors. Observation platforms included small ships, yachts, sailing vessels and speedboats. Sighting reports were collected through forms distributed *inter alia* at various marinas and nautical clubs and via the world wide web (on the Tethys Research Institute web site). Requested information included date, time, GPS position, duration of the sighting, estimated body size of the animals, estimated group size, behaviour of the animals and their minimum dis-

tance from the boat, sea state, visibility, as well as details on the observation platform and contact information. Reliable reports by observers with extensive field experience on cetaceans as well as reports by inexperienced observers, provided that such reports were documented by videos or photos suitable for species identification, were classified as "confirmed records". Undocumented reports by inexperienced observers as well as uncertain reports were classified as "unconfirmed records".

Visual surveys of cetaceans were conducted between 2001 and 2006 within an area delimited by the Italian coast to the west, 13°29'E, 44°12'N and 45°37'N (Fig. 1). The area covered by the surveys encompasses approximately 9,500 km² of sea surface (Fig. 2). Data were obtained from the following platforms: 1) fibreglass speedboat of 7 m (eye elevation of 1.8 m); 2) oceanographic ship of 24 m (eye elevation 4.0 m); 3) oceanographic ship of 35 m (eye elevation 7.2 m); and 4) oceanographic ship of 61 m (eye elevation 12.0 m). The survey effort totalled 114 days at sea. Survey data were collected under the following conditions, qualifying "on effort": 1) daylight and long-distance visibility; 2) sea state of Douglas 1 or less; 3) swell 1 or less; and 4) survey speeds of 15–36 km h⁻¹. Binoculars were not used to look for cetaceans during navigation, but could be used to confirm species identification whenever necessary.

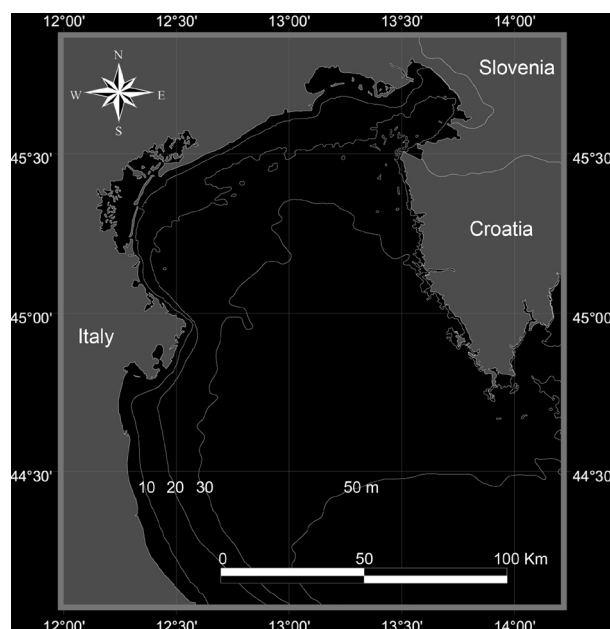


Fig. 1: Map of the upper portion of the northern Adriatic Sea, showing bathymetric contour lines.

Sl. 1: Zemljevid zgornjega dela severnega Jadranskega morja z označenimi izobatami.

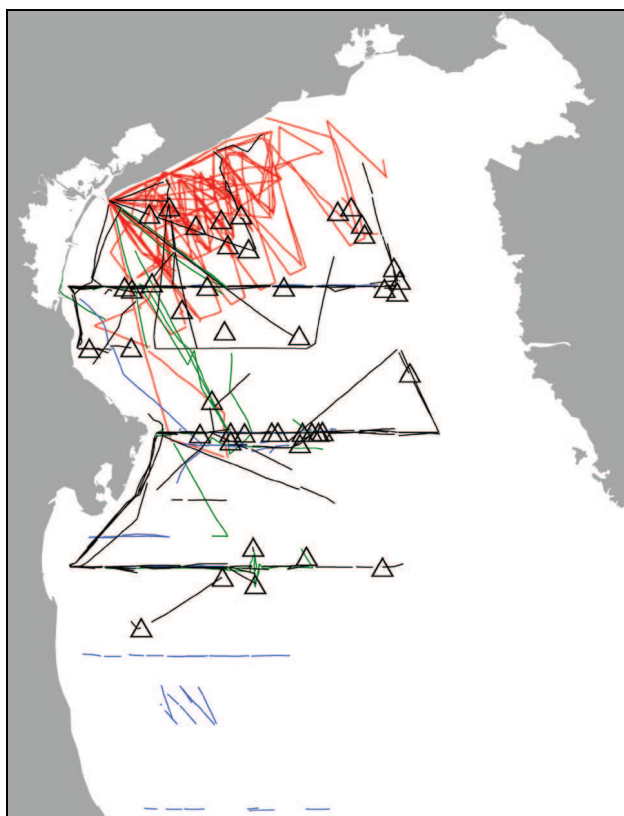


Fig. 2: Navigation "on effort" during cetacean surveys conducted between 2001 and 2006. Red line: speedboat of 7 m; green: research ship of 24 m; blue line: research ship of 61 m; black line: research ship of 35 m; triangles: position of 53 bottlenose dolphin groups sighted during navigation "on effort".

Sl. 2: Namenska plovba tekom popisa kitov in delfinov med letoma 2001 in 2006. Rdeča črta: gliser, dolg 7 m; zelena črta: raziskovalna ladja, dolga 24 m; modra črta: raziskovalna ladja, dolga 61 m; črna črta: raziskovalna ladja, dolga 35 m; trikotniki: položaj 53 skupin velikih pliskavk, opaženih med namensko plovbo.

Observation sessions were interrupted if 1) sea state, visibility or weather conditions deteriorated; or 2) the boat stopped. Sightings made off effort during cetacean surveys were not used to compute encounter rates, but were added to the dataset of opportunistic cetacean records.

Encounter rates of dolphin groups were computed based on cells of 4' latitude by 5' longitude (7,470 by 6,590 m), containing a minimum navigation "on effort" equal or greater than a cell's diagonal (9,961 m). Encounter rates were calculated by the ratio n/L , where n is the total number of sightings in a cell and L is the total number of km spent on effort in the same cell (Bearzi *et al.*, 2008).

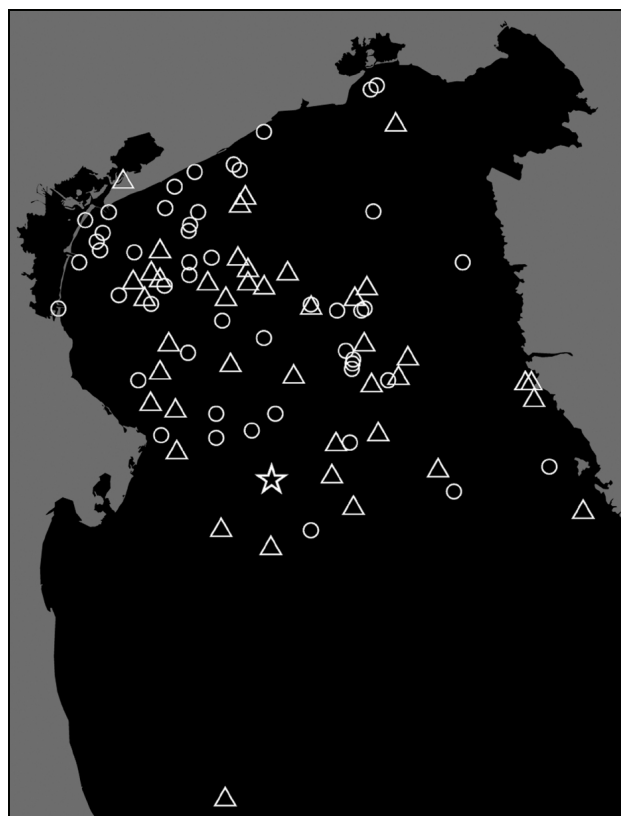


Fig. 3: Distribution of 103 sightings reported between 1988 and 2007 in the northern Adriatic Sea. Confirmed bottlenose dolphin sightings are indicated by triangles, unidentified small Delphinidae by white dots. The star shows the position of an animal reported to be a "12 m long fin whale" (unconfirmed).

Sl. 3: Distribucija 103 opažanj, zabeleženih med letoma 1988 in 2007 v severnem Jadranskem morju. Potrjena opažanja velike pliskavke so označena s trikotniki, opažanja neidentificiranih malih primerkov delfinov pa z belimi pikami. Zvezda prikazuje pozicijo živali, opisano kot "12-metrski brazdasti kit" (nepotrjeno).

RESULTS

A total of 103 cetacean sighting reports were obtained. Of these, all of the 44 confirmed records involved bottlenose dolphins. The remaining 59 unconfirmed records involved unidentified small Delphinidae that were most likely to be bottlenose dolphins, but could also include other species. There was a single observation of a large cetacean reported to be a "12 m long fin whale *Balaenoptera physalus*", sighted in 1993. The position of all the sighting reports obtained opportunistically, as well as of 33 sightings recorded off effort during cetacean surveys, is shown in figure 3. Cetacean surveys yielded an additional 53 sightings on effort, all of which were of bottlenose dolphins (Fig. 2).

Tab. 1: Survey effort, number of sightings and encounter rates of bottlenose dolphins during cetacean surveys (2001–2006).**Tab. 1: Podatki o popisu, številu opažanj in stopnji srečevanj velikih pliskavk tekom popisa kitov in delfinov (2001–2006).**

	2001	2002		2003		2004	2005	2006
	Speed-boat	Speed-boat	Research ship	Research ship	Research ship	Research ship	Research ship	Research ship
Boat length (m)	7	7	24	61	35	35	35	35
Eye elevation (m)	1.8	1.8	4.0	12.0	7.2	7.2	7.2	7.2
Survey speed (km/h)	15–36	15–36	15–18	15–24	15–24	15–24	15–24	15–24
Navigation "on effort" (km)	1591	794	548	342	290	376	536	347
Sightings total	4	7	7	12	12	10	19	15
Sightings "on effort"	3	6	5	9	6	6	9	9
Encounter rate / 100 km	0.42	0.65	0.67	1.67	0.84	1.42	1.02	0.82
SD	1.757	2.153	2.092	3.131	2.784	3.299	2.700	2.605
SE	0.311	0.393	0.427	1.107	0.839	0.778	0.697	0.824
N (cells sampled)	32	30	24	8	11	18	15	10

Navigation "on effort" during cetacean surveys totalled 4,824 km. Encounter rates of bottlenose dolphins obtained from different observation platforms are shown in Table 1. Encounter rates were not merged because of the considerable heterogeneity in vessel kind, speed, eye elevation and/or geographic distribution of the survey effort. The elevation of observers' eyes resulting from the different deck heights of survey platforms is an important factor affecting encounter rates, the probability to spot dolphins from small speedboats being generally lower than that of seeing the animals from the upper deck of oceanographic ships. While encounter rates in this study did not show significant differences according to eye elevation of observers (Kruskal-Wallis $H = 1.65$, $p = 0.65$, $df = 3$, $n = 148$), a trend was apparent and the correlation between encounter rates and eye elevation was rather strong ($R^2 = 0.9337$; Fig. 4). Encounter rates obtained with consistent methods showed some variability. For instance, encounter rates recorded between 2003 and 2006 from the same oceanographic ship (eye elevation 7.2 m) ranged between 0.82 and 1.42 groups per 100 km of navigation. However, there were no significant differences for either of the two platforms used in multiple years (35-m ship_{2003–2006}: Kruskal-Wallis $H = 0.431$, $p = 0.93$, $df = 3$, $n = 54$; speedboat_{2001–2002}: Kruskal-Wallis $H = 0.023$, $p = 0.88$, $df = 1$, $n = 62$).

DISCUSSION

This study complements existing knowledge on cetaceans in the northern Adriatic Sea. Bottlenose dolphins were the only cetacean species observed over a total of 97 confirmed sightings recorded in the study area across 20 years (1988–2007). Sighting reports and visual surveys yielded no sightings of short-beaked common dolphins, further confirming that this species is no longer a

regular component of the northern Adriatic fauna. These findings are consistent with changes occurred since 1960s, having resulted in almost exclusive presence of bottlenose dolphins (Bearzi *et al.*, 2004; Genov *et al.*, 2008). While several cetacean species have been recorded over the past decades in this part of the northern Adriatic Sea (Krystufek & Lipej, 1993; Bearzi *et al.*, 2004; Lipej *et al.*, 2004; Francese *et al.*, 2007; Genov *et al.*, 2009), none of these species were observed or confirmed during this study, apart from a single unconfirmed sighting of a fin whale.

Comparisons among encounter rates obtained in this study are not straightforward, due to heterogeneity in research platforms and methodology (Tab. 1, Fig. 4). The fact that encounter rates from small boats were generally lower than those obtained from the upper deck of large ships does not surprise, because chances of spotting dolphins at sea are expected to increase with observer's height (Buckland *et al.*, 1993).

While encounter rates of bottlenose dolphins obtained with consistent methodology did not show significant inter-annual variations, a greater effort and sample size would be needed to detect changes in distribution occurring annually or seasonally across subareas. The northern Adriatic Sea is characterised by high annual and seasonal variability of hydrological and biological variables (Franco & Michelato, 1992; Socal *et al.*, 2002; Grilli *et al.*, 2005) and its local ecosystem is especially sensitive to seasonal and long-term variations of both climate and anthropogenic nutrient loads (Degobis *et al.*, 2000; Russo *et al.*, 2002). Changes in dolphin distribution over time have been inferred to occur as a result of changes in hydrological and physiographical variables, likely to determine shifts in prey distribution (Bearzi *et al.*, 2008).

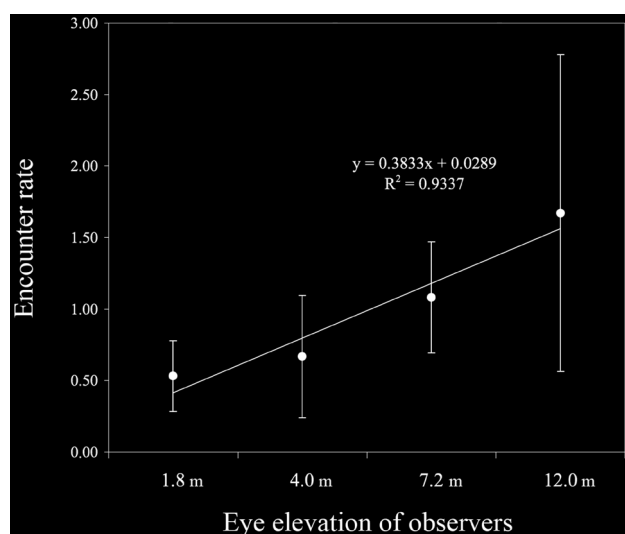


Fig. 4: Correlation between encounter rates and eye elevation of observers standing on the deck of four survey platforms used during this study. Error bars show standard errors.

Sl. 4: Korelacija med stopnjo srečevanj in višino oči opazovalcev, stojećih na štirih različnih opazovalnih ploščadih, uporabljenih v tej raziskavi. Stolpci označujejo standardne napake.

Bottlenose dolphins seemed to occur throughout the continental shelf waters covered by this study, both in-shore and offshore. However, the results of this study suggest that encounter rates of dolphins in this part of

the Adriatic may be expected to be generally low as well as variable. This information can be relevant in the future planning of dedicated aerial and ship surveys aimed to monitor cetacean abundance and trends, e.g. through distance sampling methods (Buckland *et al.*, 1993). Ships offering appropriately high observation decks should be used in order to increase encounter rates and, hence, sample size. Given that bottlenose dolphins are virtually the only species regularly found in this area, and species identification from above would not be an issue, aerial surveys may yield cost-effective information on distribution and abundance.

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PODATKI O DELFINIH IN STOPNJI SREČEVANJ S TO VRSTO V SEVERNEM JADRANSKEM MORJU MED LETOMA 1988–2007

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POVZETEK

Med letoma 1988 in 2007 smo v severnem Jadranskem morju zabeležili skupno 156 opažanj kitov in delfinov. Potrjene identifikacije ($n = 97$) so se nanašale izključno na velike pliskavke *Tursiops truncatus*. Navajamo tudi stopnjo srečevanj za to vrsto; podatki so bili pridobljeni med letoma 2001 in 2006 tekom vizualnega popisa kitov in delfinov z različnih raziskovalnih plovil med 4824 km dolgo namensko plovbo po območju velikem cca. 9,500 km². Stopnja srečevanj se je gibala med 0,42 in 1,67 skupin na 100 km plovbe, brez izrazite razlike v letih, pod pogojem

uporabe konsistentne metodologije. Ugotovljena je bila korelacija med stopnjo srečevanj in višino oči opazovalca, odvisno od različnih višin opazovalnih ploščadi. Izsledki te študije kažejo na to, da je velika pliskavka glavna vrsta kitov in delfinov, ki se tekom zadnjih 20 let redno pojavlja v severnem Jadranskem morju. Te informacije prispevajo k oblikovanju okoljskih izhodišč, lahko pa se uporabijo tudi pri oblikovanju popisov za pridobivanje absolutne ocene številčnosti kitov in delfinov v tem delu Jadranskega morja.

Ključne besede: kiti in delfini, Jadransko morje, velika pliskavka, *Tursiops truncatus*

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FIRST RECORD OF THE AFRICAN HIND (*CEPHALOPHOLIS TAENIOPS*) (PISCES: SERRANIDAE) IN THE LEVANT

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ABSTRACT

The African hind Cephalopholis taeniops was recorded for the first time in the Levant. This species was known hitherto only from the eastern Atlantic Ocean from Morocco to Angola and southern Mediterranean coast of Libya.

Key words: African hind, *Cephalopholis taeniops*, Mediterranean, Levant, first record

PRIMA SEGNALAZIONE DI CERNIA ATLANTICA (*CEPHALOPHOLIS TAENIOPS*) (PISCES: SERRANIDAE) NEL BACINO LEVANTINO

SINTESI

La presenza della cernia atlantica Cephalopholis taeniops è stata confermata per la prima volta nel Bacino Levantino. Finora la specie era conosciuta solo per la parte orientale dell'oceano Atlantico dal Marocco all'Angola, e per la costa mediterranea meridionale della Libia.

Parole chiave: Cernia atlantica, *Cephalopholis taeniops*, Mediterraneo, Bacino Levantino, prima segnalazione

INTRODUCTION

In the Mediterranean new fish records are continually being discovered and have increased in recent decades. Although the majority of the new arrivals have originated from the Red Sea ("Lessepsian migrants"), there are a number of migrant species of Atlantic origin (Golani *et al.*, 2002, 2004).

Unlike Lessepsian migrants that usually establish sustainable populations in the Mediterranean, whether gradually or immediately upon arrival, most of the recently recorded species of Atlantic origin remain rare or are considered vagrant in their new habitat. However, there are two notable exceptions to this general rule. The puffer fish *Sphoeroides pachygaster* (Müller and Troschel, 1848) was first recorded in the Mediterranean near Mallorca (Oliver, 1981) and within a decade reached the coast of Israel (Golani, 1996). The other example is the Least Amberjack *Seriola fasciata* (Bloch, 1793) that was first recorded in the Mediterranean from the Balearic Islands (Massutí & Stefanescu, 1993) and a decade later became a successful commercial species in the central Mediterranean (Andaloro *et al.*, 2005); a few years later, it reached the Levant (Sonin *et al.*, 2009).

In this paper, we report the occurrence of the African Hind (*Cephalopholis taeniops*) from the Israeli Mediterranean coast. This constitutes a significant distribution extension of this species in the Mediterranean.

MATERIAL AND METHODS

On 23 June 2009, a 236 mm Standard Length (291 mm Total Length) specimen of *Cephalopholis taeniops* (Valenciennes, 1828) (Fig. 1) was collected using a spear-gun in a rocky habitat at depths of 30 m in the vicinity of Haifa Bay (Fig. 2). The specimen was fixed in

10% formaldehyde, later transferred to 70% alcohol and deposited in the Hebrew University Fish Collection (HUJ) with the catalogue number 19841. Measurements and counts followed Hubbs & Lagler (1947). Gill rakers on the first left arch were counted. The last dorsal and anal rays, which are divided almost to the base, were considered to be one ray.

RESULTS AND DISCUSSION

The body is robust and slightly compressed, the depth at the origin of dorsal fin (35.9%), large head (39.7%), predorsal (40.2%), preanal (67.0%), least caudal peduncle (13.7%); all proportions are given as a percentage of Standard Length. A small eye (14.1%), slightly concaved interorbital (16.5%), jaw (48.6%) reaching back to the posterior third of the eye, the snout (26.0%); all proportions are given as a percentage of Head Length. The dorsal fin is continuous, with 9 spines and 16 soft rays; the anal fin with 3 spines and 8 soft rays; the pectoral fin is round, with 17 rays on both sides; the pelvic fin is also round, with 1 spine and 5 rays; and the caudal fin also round.

The posterior nostril is close to the eye at the level of the upper third, and the anterior nostril is very close and slightly lower, equipped with a small flap.

The mouth is large, lower jaw projected. There are two strong canines at the anterior of each jaw. At the base between the canines of the upper jaw, there is a patch of sharp teeth of different sizes; the inner teeth are the largest. There is also a band of small sharp teeth on the upper jaw becoming narrow posteriorly; a patch of fang-like teeth at the lower jaw becoming smaller towards its posterior end; a small overturned shallow V-shaped vomer patch with small sharp teeth; a pair of palatine teeth patches immediately posterior to the vo-



Fig. 1: *Cephalopholis taeniops*, 236 mm Standard Length, Haifa Bay, Israel, HUI 19841.
Sl. 1: *Cephalopholis taeniops*, 236 mm standardne dolžine, zaliv Haifa, Izrael, HUI 19841.

mer patch, equipped with small sharp teeth. There are 4 knob-like undeveloped and 4 developed gill rakers on the upper arch and 3 knob-like undeveloped and 12 rakers on the lower arch. Three flat spines on the posterior margin of the operculum, the distance between the central spine to the upper spine is almost twice that to the lower spine. The preoperculum is delicately serrated at its lower margin.

Color of the fresh specimen. The body is red-orange, covered with numerous light blue spots surrounded with black margins. The posterior part of all fins is slightly darker; the posterior margin of caudal fin has a faded light blue margin. There is an almost horizontal bluish line surrounded with a black line under the eye. A blue ring with a dot in the center, both surrounded with black at the ventral edge of the operculum slightly behind the posterior end of the premaxilla. The eye is red with a black pupil.

Color of the preserved specimen after one week in formaldehyde. The body is yellowish to beige with black dots.

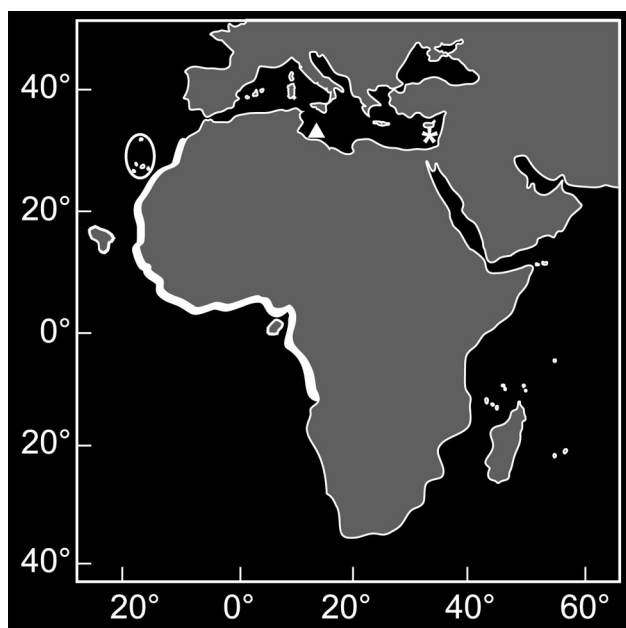


Fig. 2: Map of Africa and the Mediterranean showing the original distribution of *Cephalopholis taeniops* (—), region of previous records in the Mediterranean (▲) and the present study (*).

Sl. 2: Zamljevid Afrike in Sredozemlja, na katerem je označena prvotna razširjenost *Cephalopholis taeniops* (—), področje dosedanjega pojavljanja v Sredozemlju (▲) in pričujoče raziskave (*).

All counts and measurements agree with the description of *C. taeniops* given by Smith (1981), Serret & Opic (1990), Heemstra & Randal (1993) and Ben Abdallah *et al.* (2007).

Originally, *C. taeniops* was known from western Africa, from Morocco to Angola. It was first recorded in the Mediterranean off the coast of Libya by Ben Abdallah *et al.* (2007) reporting two specimens collected from the Gulf of Syrte, one off Tripoli (September 2002) and the second from Missurata, ca. 200 km east of Tripoli (June 2004). In the subsequent years another four specimens were collected in the coastal waters of Libya (A. Ben Abdallah, *pers. comm.*).

This report constitutes the first record of this species from the Levant extending its known distribution significantly eastward by ca 1800 km. The records of several specimens in the Mediterranean over a period of nine years suggest that *C. taeniops* has established a sustainable population in its new region.

C. taeniops can be distinguished from its co-familial species in the Mediterranean by its unique coloration. The color pattern of *C. taeniops* is similar to that of the Indo-Pacific *Cephalopholis miniata* (Forsskål, 1775) which is found also in the Red Sea. However, *C. taeniops* has a clear horizontal line under its eye, as well as a blue ring on the lower part of the operculum, distinguishing it from *C. miniata*.

C. taeniops is a carnivorous fish inhabiting rocky and sandy substrates. It reaches a Total Length of 40 cm. It is considered to be an esteemed commercial species generally caught with long-line and trawl; some of the West African catch is marketed in Europe.

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We would like to thank Mr. S. Naima for providing the specimen.

PRVI PODATEK O POJAVLJANJU KIRNJE VRSTE *CEPHALOPHOLIS TAENIOPS* (PISCES: SERRANIDAE) V LEVANTSKEM MORJU

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POVZETEK

Prvič je zabeleženo pojavljanje kirnje vrste *Cephalopholis taeniops* v Levantskem morju. Vrsta je bila dosedaj znana samo za vzhodno atlantsko obalo od Maroka do Angole in južno Sredozemlje ob obali Libije.

Ključne besede: kirnja, *Cephalopholis taeniops*, Sredozemlje, Levantsko morje, prvo pojavljanje

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THE MEAGRE *ARGYROSUMUS REGIUS* (ASSO, 1801), IN CROATIAN WATERS (NERETVA CHANNEL, SOUTHERN ADRIATIC): RECOVERY OF THE POPULATION OR AN ESCAPE FROM MARICULTURE?

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ABSTRACT

The meagre specimen (total length TL = 57.4 cm, weight W = 1493.8 g, ♀) was caught by gill-net on 9th August 2008 near the village Blaca (the southern Adriatic, Croatian coast) at the depth of 10 m on rocky-muddy bottom. It seems that we are dealing with the case of an escape from mariculture, especially if we take into account the general look and condition of the caught specimen.

Key words: *Argyrosomus regius*, occurrence, status, Croatian waters, Adriatic Sea

BOCCA D'ORO *ARGYROSUMUS REGIUS* (ASSO, 1801) IN ACQUE CROATE (CANALE DI NERETVA, ADRIATICO MERIDIONALE): RICUPERO DI UNA POPOLAZIONE O FUGA DA MARICOLTURA?

SINTESI

Un esemplare di Bocca d'oro (lunghezza totale TL = 57,4 cm, peso W = 1493,8 g, ♀) è stato catturato con un tramaglio il 9 agosto 2008 vicino al villaggio di Blaca (Adriatico meridionale, costa croata), ad una profondità di 10 metri, su substrato roccioso-melmoso. Sembra che si tratti di un esemplare scappato da maricoltura, specialmente se viene considerata l'apparenza generale e le condizioni del pesce catturato.

Parole chiave: *Argyrosomus regius*, ritrovamento, stato, acque croate, mare Adriatico

INTRODUCTION

The meagre, *Argyrosomus regius* (Asso, 1801) is distributed in the Eastern Atlantic, from Norway to Gibraltar and Congo, including the Mediterranean and the Black Sea. It migrated to the Red Sea via the Suez Canal (Chao & Trewavas, 1990). It inhabits inshore and shelf waters, moves close to the bottom as well as in surface and mid-waters, pursuing shoals of clupeids and mulgils and congregates inshore to spawn during spring and summer. Juveniles and sub-adults enter estuaries and coastal lagoons (Chao & Trewavas, 1990). Both adults and juveniles are migratory, moving along shore or offshore-onshore in response to temperature change (Griffiths & Heemstra, 1995). It feeds on fish and swimming crustaceans.

There are no data (biology, ecology) available on this species in Croatian waters (the eastern Adriatic). The aim of this paper is to present data regarding the record of the meagre specimen in Croatian waters and its morphometric and meristic characters.

MATERIAL AND METHODS

The meagre specimen (total length TL = 57.4 cm, weight W = 1493.8 g, ♀) was caught by gill-net ("baracuda" net) on 9th August 2008 near the settlement Blaca (the River Neretva and Mala Neretva estuaries, the southern Adriatic, Croatian coast) at the depth of 10 m on rocky-muddy bottom (Fig. 1). The specimen was identified according to Jardas (1996). It was subsequently measured to the nearest 0.1 cm and weighed to the nearest 0.1 g. The meristic characters considered were dorsal, anal and pectoral fins. The condition factor (CF) was calculated as $CF = W \times 100/L^3$.

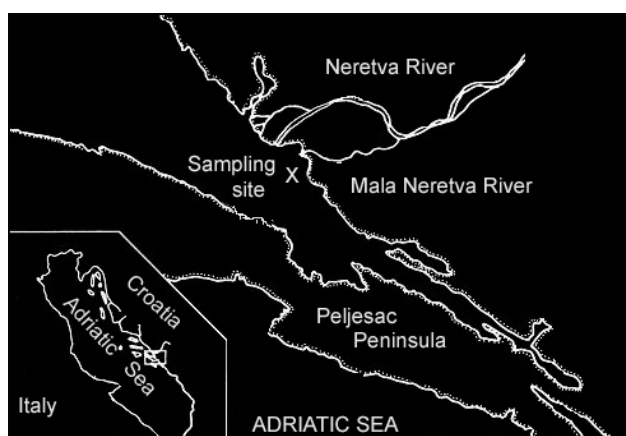


Fig. 1: Sampling site where the meagre specimen was caught (Neretva channel, the southern Adriatic)

Sl. 1: Vzorčno mesto, kjer je bil ujet primerek grbe (Neretvanski kanal, južno Jadransko morje).

The specimen is deposited in the Collection of the Department for Aquaculture, University of Dubrovnik, Croatia (Fig. 2).

RESULTS AND DISCUSSION

In Table 1, the main morphometric and meristic data are given (first data for the meagre for Croatian waters). The meristic characteristics are in agreement with data by Jardas (1996), i.e. D1: IX-X, D2: I+26-29, A: II+7-8, P: 16-17, V: I+5.

Description of the Adriatic specimen

The body is elongate, nearly fusiform; the mouth large, oblique and terminal: the teeth in upper jaw villiform in narrow bands, the outer row is slightly enlarged; the lower jaw teeth in 3 irregular rows. Three small upper pores and five marginal ones on snout. The caudal fin truncate to S-shaped. Scales are ctenoid, some cycloid scales on chest, snout and below eyes. Body colour is silvery, a little bit darker on the back, with bronze reflections on sides. The fins are greyish, while the inside of the mouth is yellowish-orange.

Tab. 1: Morphometric (in cm) and meristic data of the meagre specimen (♀) in the southern Adriatic.

Tab. 1: Morfometrični (v cm) in meristični podatki o primerku grbe (♀) v južnem Jadranskom morju.

Weight (W, g)	1493.8
Morphometric characters (cm)	
Total length (TL)	57.4
Standard length (SL)	47.8
Pre-anal length (Lpa)	32.2
Pre-dorsal length (Lpd)	15.1
Pre-pelvic length (Lpl)	15.5
Pre-pectoral (Lpp)	14.5
Body depth	12.5
Head length (HL)	14.1
Eye diameter (O)	2.5
Pre-orbital length (Po)	3.8
Meristic characters	
Dorsal fin (D1)	X
Dorsal fin (D2)	I+27
Pectoral fin (P)	16
Ventral fin (V)	I+5
Anal fin (A)	II+7
Scales in <i>linea lateralis</i>	53

Several authors (Šoljan, 1975; Jardas, 1985, 1996) treated this species as rare or very rare in the Adriatic Sea. According to fishermen reports and some publications (Jardas, 1996), this species almost disappeared from its habitats, sandy and muddy shallows with turbid

waters, near river mouths, or even in freshwater (the River Cetina and the River Neretva, in Croatian waters). According to some indicies, the region of Ulcinj (Montenegro) by the mouth of the River Bojana is probably the last location in the Adriatic Sea where it can be observed by several specimens per year (Joksimović, 2007). Jardas *et al.* (2008) list this species as regionally extinct species in the Red Book of Sea Fishes of Croatia. As already mentioned, the record of the meagre specimen was surprising, emphasizing the question whether the finding of the specimen means a renewal of the population of this species or is this quite another matter; it is possible that the statement of Jardas *et al.* (2008) is incorrect or we can be dealing with a possible escape from mariculture.

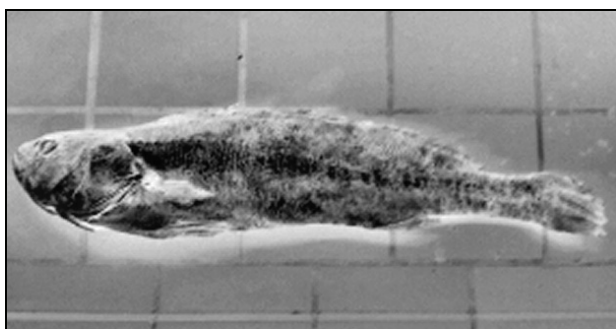


Fig. 2: The meagre specimen (TL = 57.4 cm).
Sl. 2: Primerek grbe (TL = 57,4 cm).

The condition factor of the caught meagre specimen was low (CF = 0.790), pointing to the fact that the feeding activity was probably limited (stomach of specimen was empty). Significant number of specimens of similar characteristics were caught and sold by local fishermen, but these specimens were unavailable to us, hence not verified on the scientific base. We interviewed the owners of fish farms in adjacent Mali Ston Bay and the owner of "Karaka" Ltd. Company from Neum (Bosnia and Herzegovina) and they confirmed the escape of around 400 specimens of meagre from their cages. The origin of meagre juveniles is a hatchery in France.

The record of the caught meagre seems to be the case of an escape from mariculture, especially if we take into account the general look and condition of the specimen. Some similar cases have been reported for *Dicentrarchus labrax*, *Sparus aurata* and *Pagrus major* on several locations in the eastern Adriatic (Dulčić & Kraljević, 2007; Glamuzina & Dulčić, 2008). In the last ten years gilthead sea bream, *S. aurata* established strong population in this area, similarly based on escapes from fish farms (Glamuzina & Dulčić, 2008). If this scenario happens with meagre, we may expect recovery of the population and establishment of a wild population based on aquaculture activities. Therefore, the status of meagre in Croatian waters needs to be evaluated on a continuous basis.

GRBA *ARGYROSUMUS REGIUS* (ASSO, 1801) V HRVAŠKIH VODAH (NERETVANSKI KANAL, JUŽNO JADRANSKO MORJE): OBNOVA POPULACIJE ALI POBEG IZ MARIKULTURE?

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POVZETEK

Primerek grbe (celotna dolžina TL = 57,4 cm, teža W = 1493,8 g, ♀) je bil ujet z zabodno mrežo 9. avgusta 2009 blizu vasi Blaca (južni Jadran, hrvaška obala) v globini 10m na skalnato blatnem dnu. Zdi se, da gre za primer pobega iz marikulture, še posebej če upoštevamo splošni izgled in stanje ujetega primerka.

Ključne besede: *Argyrosomus regius*, pojav, status, hrvaške vode, Jadransko morje

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THE DIET OF THE RAVEN *CORVUS CORAX* IN SOUTH-WEST SLOVENIA

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ABSTRACT

The diet of the raven was investigated in 2008 in south-west Slovenia. 158 food items, belonging to 26 different food groups, were retrieved from 60 whole and some broken pellets collected during the spring and autumn. Vertebrate remains were found in 57 pellets and plant debris in 53 pellets. Sheep remains were found in 32 pellets, and were significantly more common in pellets from sheep pastures than from areas with no pastures. Deer, invertebrate and bird remains were scarce.

Key words: the raven, *Corvus corax*, diet, south-west Slovenia

DIETA DEL CORVO IMPERIALE *CORVUS CORAX* IN SLOVENIA SUD-OCCIDENTALE

SINTESI

Gli autori hanno studiato la dieta del Corvo imperiale nel 2008 nella Slovenia sud-occidentale. 158 pezzi di cibo, appartenenti a 26 differenti gruppi alimentari, sono stati recuperati da 60 borre intere ed alcune danneggiate, raccolte durante la primavera e l'autunno. Resti di vertebrati sono stati ritrovati in 57 borre, mentre resti vegetali in 53 borre. Resti di pecora sono stati riscontrati in 32 borre, risultando significativamente più comuni nelle borre raccolte sui pascoli ovinici che in quelle raccolte nelle aree lontane dai pascoli. Resti di cervidi, invertebrati e uccelli sono risultati scarsi.

Parole chiave: Corvo imperiale, *Corvus corax*, dieta, Slovenia sud-occidentale

INTRODUCTION

The raven population (*Corvus corax*) consists of birds with two types of social behaviour: breeding birds, which appear to be territorial and live in pairs, and non-breeding, non-territorial birds, which live year-round in flocks (Ratcliffe, 1997). The raven population in Slovenia is estimated at 2000 to 3000 breeding individuals (1000 to 1500 breeding pairs; Geister, 1995) and at least 1500 to 3000 non-breeding individuals (Tome *et al.*, 2009). Although no quantitative data exists, there are some clues that the population has increased in recent decades (Tome *et al.*, 2009). This increase is consistent with observations all over Europe (BirdLife international, 2004; EBCC 2008) and is thought to be the result of the ban on shooting in some countries and increase of sheep farming practice in others (Tome *et al.*, 2009). The population size of ravens is known to correlate with the extent of sheep farming (Newton *et al.*, 1982).

The raven is first of all a scavenger and, as such, a vulture substitute in northern Europe (Ratcliffe, 1997). It feeds on dead animals from the size of a mouse to a whale. It can also be a predator, catching live prey. The extent to which it attacks live animals depends on the amount of available carrion. Rabbits are usually considered to be the biggest animals that ravens can successfully prey on, but then only if they are cornered or if their defence is disabled in some other way.

A common belief among farmers is that ravens kill sheep for food, especially lambs. The question of lamb killing (also calf killing) has been addressed by scientists several times (Ratcliffe, 1997; Langgemach *et al.*, 1995; Wallschläger *et al.*, 2004; Glandt, 2008), but only rarely hard evidence for successful predation was established. Even then, as found later, the animal under attack had ill developed internal organs or was affected by a potentially deadly disease. On the other hand, a lot of proof of ravens feeding on sheep carcasses has been established. Nevertheless ravens still have a bad reputation as large scale sheep killers.

The main aim of this work is to present the diet of the raven in south-west Slovenia, as derived from pellet analysis. Although raven diet studies are not rare, especially from England and Ireland (Marquiss *et al.*, 1978; Ewins *et al.*, 1986; Marquiss & Booth, 1986; Berrow, 1992), this is the first study of this kind from this part of Europe. It should be noted that the results cannot be taken as an arbiter of raven's guilt or innocence as a sheep killer, as they provide no information about predation and potential killing behaviour. Sheep remains in the raven's diet in this study are solely a sign of the bird feeding habits.

MATERIALS AND METHODS

Study area

We collected pellets from two areas in south-west Slovenia. The first was located in the Karst region near the settlements of Sežana, Divača and Kozina (squares on Fig. 1). Pellets were collected from and under the cliffs in rocky depressions, where raven nests were located. These localities were surrounded by forests or overgrown meadows and there were no pastures within at least a kilometre.

The second area comprised sheep pastures at Volovja reber and Gure above Ilirska Bistrica (triangles on Fig. 1). We collected pellets under the trees and rocky outcrops within or close to pastures, where raven flocks were often spotted. We were not aware of any raven nests in this area. We estimate that pellets from both areas were not older than two months on the day of collection.

Materials and methods

The content of the pellets was analyzed in the laboratory. Pellets were soaked in water for ca. 15 minutes and then washed with tap water on a 0.5 mm mesh sieve. Material remaining on the sieve was dried and inspected macroscopically and, if needed, also under 100–400x magnification. The volume proportion of each food item found in a pellet was estimated visually. From each pellet we collected approx. 20 guard hairs and 5 feathers (when present), put them in 96% ethanol for approx. 30 minutes to clean, and let them dry. Macroscopic (general form, size, colour, rigidity, shape of the apex) and microscopic (structure and pattern of cuticular scales, shape of the cross-section, shape and size of the medullary space) characteristics of hairs were noted. The microstructure of the cuticle was inspected using cuticular imprints on celluloid plates. Species determination was performed according to Day (1966), Teerink (1991), Meyer *et al.* (2002) and with the comparative material stored at the Department of Biology at the University of Ljubljana. Teeth and bone remains of small mammals were identified according to Kryštufek (1985, 1999) and with the comparative osteological material. Remains of bats were analysed by a specialist. Plant material was separated into green or wooden material, fruits and seeds. When possible we determined the plants more precisely.

Due to intensive digestion in the stomach, some food remains from pellets were in a very poor condition, and impossible to determine to a species level. For that reason the term food item in this text refers to the part of the material from one pellet belonging to a particular species, genus, family or class, whichever level of determination was the lowest possible.

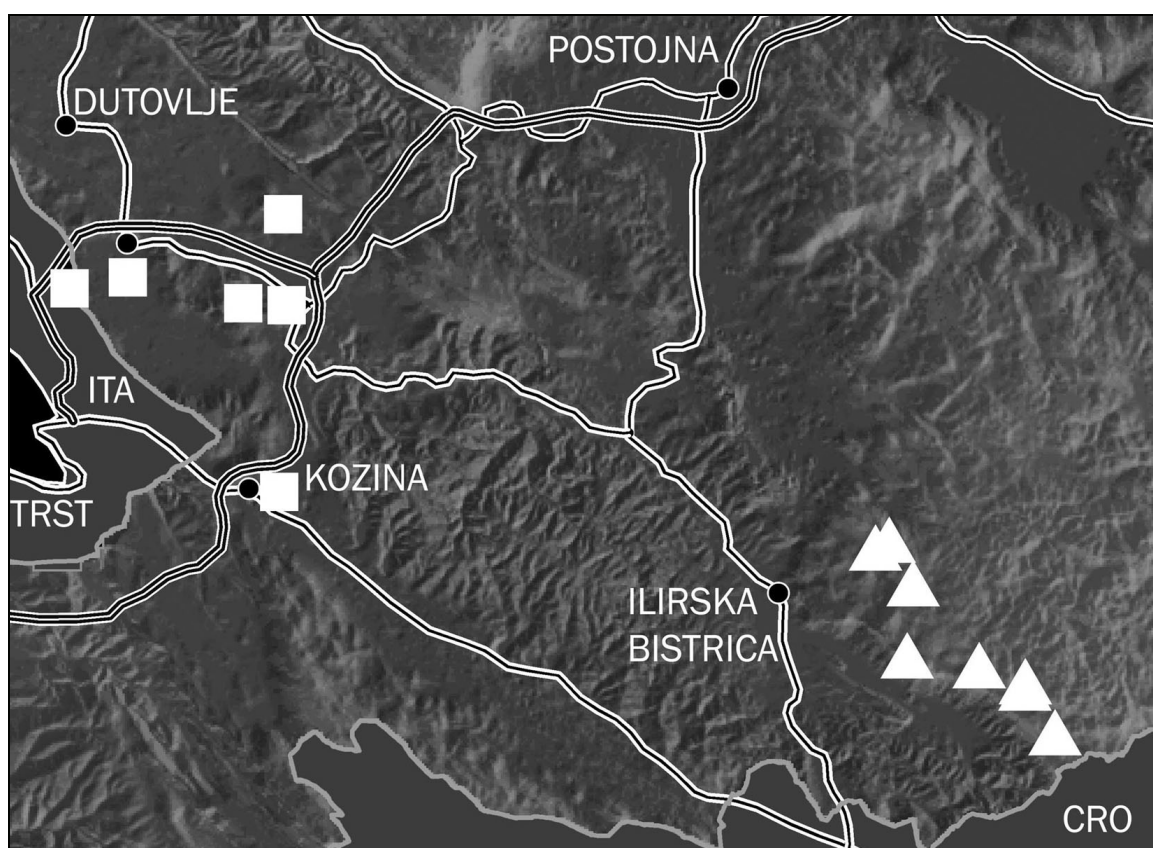


Fig. 1: Study site (squares: localities of pellet collection on Karst region; triangles: localities of pellet collection on pastures).

Sl. 1: Raziskovano področje (kvadrati: lokalitete zbiranja izbljuvkov na Krasu; trikotniki: lokalitete zbiranja izbljuvkov na pašnikih).

We used four methods to present pellet analysis results: 1) frequency of occurrence, calculated as the proportion of pellets in which a food item was found; 2) proportion of occurrence, calculated as the number of pellets where a particular food item was found divided by the number of food items from all pellets; 3) volume proportion, calculated as the sum of the volume proportions of a particular food item in pellets divided by the total number of pellets, and 4) average volume proportion, calculated as the sum of the volume proportion of a particular food item in pellets divided by the number of pellets including this food item only.

All pellets were analyzed by the same person (MK) to minimize variability caused by observer-related errors. We climbed the nests to collect the pellets only after the nestlings were fledged.

RESULTS

Food remains were analyzed in 60 whole raven pellets and some broken pellet material from 13 locations. Spring samples (15 pellets) were collected from 9th to 13th May 2008 in the Karst region only, autumn samples (45 pellets) from 11th September to 15th October 2008 in pastures. 158 food items, belonging to 26 different food groups, were separated from pellets. In single whole pellets we found one to five food items, on average 2.4 food items per pellet (s.d. = 0.85).

Vertebrate remains were found in 57 whole pellets (95%), and plant remains in 53 whole pellets (88%). Sheep remains were found in 32 whole pellets (53%), while remains of other domesticated animals were scarce. Small mammals were also relatively common, followed by deer, birds and invertebrates. Green plant material was the most common plant food item, followed by fruits and seeds (Tab. 1).

Tab. 1: Diet composition of ravens in SW Slovenia (N of all food items is 158).**Tab. 1: Sestava prehrane krokarjev v JZ Sloveniji (N vseh enot hrane je 158).**

Food item	N of food items	Frequency of occurrence	Proportion of occurrence	Volume proportion	Average volume proportion
animals	78	0.919	0.494	0.548	0.436
Vertebrata	71	0.919	0.449	0.518	0.452
Mammalia	65	0.887	0.411	0.450	0.429
Cervidae	7	0.113	0.044	0.054	0.476
Carnivora	4	0.065	0.025	0.021	0.333
undet. large mammals	4	0.065	0.025	0.016	0.255
domesticated ungulates	36	0.581	0.228	0.228	0.393
sheep	32	0.516	0.203	0.224	0.434
goat	2	0.032	0.013	0.002	0.050
pig	1	0.016	0.006	0.002	0.100
horse	1	0.016	0.006	0.001	0.050
small mammals	14	0.210	0.089	0.130	0.575
<i>Myotis myotis</i>	2	0.032	0.013	0.020	0.625
Muridae	2	0.032	0.013	0.010	0.325
Gliridae	2	0.032	0.013	0.021	0.650
<i>Talpa europaea</i>	1	0.016	0.006	0.015	0.900
undet. small mammals	7	0.113	0.044	0.064	0.564
Aves	6	0.097	0.038	0.068	0.703
Passeriniiformes	3	0.048	0.019	0.034	0.700
Falconiformes	1	0.016	0.006	0.008	0.520
undet. birds	2	0.032	0.013	0.026	0.800
Invertebrata	7	0.113	0.044	0.030	0.269
Coleoptera	3	0.048	0.019	0.021	0.440
Saltatoria	1	0.016	0.006	0.008	0.500
undet. insects	2	0.032	0.013	0.000	0.015
snails	1	0.016	0.006	0.000	0.030
plants	67	0.806	0.424	0.433	0.401
green plant material	40	0.645	0.253	0.306	0.475
fruit	1	0.016	0.006	0.016	1.000
cereals	1	0.016	0.006	0.016	1.000
corn	2	0.032	0.013	0.014	0.425
undet. fruits and seeds	18	0.290	0.114	0.075	0.257
wooden plant material	5	0.081	0.032	0.006	0.078
stones	10	0.161	0.063	0.009	0.057
undetermined	3	0.048	0.019	0.009	0.193

Sheep remains were significantly more common in pellets found in the area with sheep pastures than in those in the area with no pastures. Ravens distant to pastures fed more on fruits, seeds, small mammals and large wild mammals. There was also a significant difference in the proportion of bird remains between two areas. Very few were found in pellets from pastures, but rather more in pellets found in areas where sheep were not available as food (Tab. 2).

DISCUSSION

None of the quantitative measures of the raven diet in this study (frequency of occurrence, proportion of oc-

currence, volume proportion) are directly proportional to the real quantities of food ingested. For example, sheep remains from pellets in one locality could have arisen from one or from several animals; ravens could have eaten a whole sheep or only a part of it. The amount of food remains regurgitated in pellets depends on the degree of digestion, which is different for different items. So the results do not provide an exact picture of the diet. They are probably quite accurate in presenting its qualitative composition, but only provide an approximate indication of the importance of particular food items.

Tab. 2: Diets of ravens dwelling near and far from sheep pastures. Numbers are proportions of the occurrence in pellets, the difference is denoted using Chi-square test (* $p < 0.05$; ** $p < 0.01$).

Tab. 2: Prehrana krokarjev, živečih blizu in daleč stran od ovčjih pašnikov. Številke predstavljajo delež pojavljanja v izbljuvkih, razlika je označena s testom hi-kvadrat (* $p < 0,05$; ** $p < 0,01$).

Prey category	Sheep pastures far	Sheep pastures near	Chi-square
sheep	0.065	0.259	**
domesticated animal excl. sheep	0.109	0.027	*
large wildlife	0.130	0.045	
small mammals	0.152	0.063	
birds	0.109	0.009	**
invertebrates	0.065	0.036	
green plant material	0.109	0.313	*
fruits and seeds	0.174	0.125	
wood, stones, undetermined	0.087	0.125	
N food items	46	112	

Sheep carrion appears to be a frequent food item in raven pellets in south-west Slovenia, which is similar to findings of studies made elsewhere (*i.e.*, Newton *et al.*, 1982; Ewins *et al.*, 1986). In our samples from all localities, sheep remains were found in over half of the pellets. But sheep are by no means essential for the survival of ravens. Almost no sheep remains were found in pellets collected from nest sites. This indicates that even at a time of great demand for food, when adults must feed themselves and the young birds, ravens can thrive without domesticated animals as a food source, at least if they have sufficient nutritious plant material, small mammals and birds at hand, which were frequently found in those pellets.

Although in two sampling areas pellets were collected in different seasons (pellets from the Karst region in breeding season pellets above Ilirska Bistrica in post-breeding season), we argue that differences in the diet are not season related. The raven is opportunistic in its diet, exploiting whatever locally is available the most (Ratcliffe, 1997). The difference is probably mostly due to lack of sheep pastures in one and its abundance in the other area.

There is little doubt that pellets from nest sites belong to breeding ravens, adults or young fed by adults. There is also no reason not to believe that pairs with nests close to pastures have more sheep remains in the diet

than those we inspected. Less clear, however, is the social status of ravens whose pellets were found in autumn at Volovja reber and Gure. Since they were observed in groups, not in pairs, it is possible that they belong to the year-round flocks of non-breeding individuals. According to Ratcliffe (1997), breeding birds in the UK remain around the nest site in pairs throughout the year, protecting the territory, so large groups can always be considered as non-breeders. More observations on individually marked birds or even telemetry studies would be necessary to investigate whether, in Slovenia, breeding pairs join non-breeders in flocks after the breeding season. The results would be interesting from the point of view of the raven – sheep interaction. They would add some understanding to the current enigma as to which social group is responsible for ravens being on farmers' black lists: non-breeders or both non-breeders and breeders – quite possibly only the more mobile non-breeders.

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PREHRANA KROKARJA *CORVUS CORAX* V JUGOZAHODNI SLOVENIJI

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POVZETEK

V letu 2008 smo v jugozahodnem delu Slovenije raziskovali prehrano krokarjev (*Corvus corax*) na osnovi preiskave izbljuvkov. Izbljuvke smo nabirali na dveh lokacijah, na Krasu in na območju Volovje rebri in Gur pri Ilirski Bistrici. Iz 60 celih in nekaj razdrobljenih izbljuvkov smo izolirali 158 enot hrane, ki so pripadale 26 različnim taksonomskim skupinam. V 57 izbljuvkah smo našli ostanke vretenčarjev, v 53 izbljuvkah ostanke rastlinske hrane. Ostanke ovc smo odkrili v 32 izbljuvkah; značilno več v izbljuvkah nabranih v bližini ovčjih pašnikov kakor v izbljuvkah nabranih na lokacijah, ki so bile od pašnikov oddaljene. Ostanke srnjadi, jelenjadi, ptic in nevretenčarjev so bili redki.

Ključne besede: krokar, *Corvus corax*, prehrana, jugozahodna Slovenija

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ADDITIONAL RECORDS AND A NEW DESCRIPTION OF *PROTONEMURA KHROUMIRIENSIS* SP. N. (PLECOPTERA, NEMOURIDAE) FROM TUNISIA

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ABSTRACT

Protonemura khroumiriensis sp.n. has been recorded in several valleys in the Tunisian Khroumirian mountains. The species is morphologically closely related to *Protonemura ruffoi* from the *Protonemura corsicana* group, which has a Circum-Mediterranean and Caucasian distribution. Particularly the male is well distinguished by the shape of its epiproct, lack of apical appendix of the epiproct, the shape of the paraprocts and vesicle on sternite 9. The female can be distinguished by its trapezoidal subgenital plate. The subgenital plate is well sclerotized, except in the middle area. This species preferentially colonizes temporary streams and adapts its life cycle to their flowing periods. Its flight period lasts from late winter to late spring, but differs slightly from site to site.

Key words: Nemouridae, *Protonemura khroumiriensis*, Khroumirian valley, Tunisia, new species

NUOVE SEGNALAZIONI E DESCRIZIONE DI *PROTONEMURA KHROUMIRIENSIS* SP. N. (PLECOPTERA, NEMOURIDAE) IN TUNISIA

SINTESI

Protonemura khroumiriensis sp.n. è stata segnalata in diverse valli delle montagne tunisine di Khroumirian. La specie è morfologicamente strettamente legata a *Protonemura ruffoi* del gruppo *Protonemura corsicana*, che ha una distribuzione circum-mediterranea e caucasica. In particolare, il maschio si distingue bene per la forma dell'epiprocto, l'assenza dell'appendice apicale dell'epiprocto, la forma del paraprocto e la vescicola sul 9° sternite. La femmina viene distinta per la forma trapezoidale della placca subanale. Tale placca è ben sclerificata, tranne che nella parte centrale. La specie preferisce colonizzare temporaneamente corsi d'acqua ed adatta il proprio ciclo di vita ai periodi di piena. Il periodo di volo della specie va dal tardo inverno alla tarda primavera, ma può variare da sito a sito.

Parole chiave: Nemouridae, *Protonemura khroumiriensis*, valle di Khroumirian, Tunisia, nuova specie

INTRODUCTION

Stoneflies constitute a very important component of the freshwater macroinvertebrate communities. The larvae are found almost exclusively in running waters and reach their greatest diversity in small and high altitude streams. They are generally associated with coarse substrate such as cobble, leaf packs and woody debris. Plecoptera such as other orders of aquatic insects is very sensitive to the changes in water components, such as dissolved oxygen dose, mineralization of water, and pollution risks. This explains why species belonging to this order are considered good bioindicator of freshwater ecosystems. Plecoptera is one of the key taxa in many bio-index methods adopted in such studies (Alba-Tercedor & Sánchez-Ortega, 1988; Alba-Tercedor *et al.*, 2002). Stonefly adults have a very short life (1–4 weeks), compared with the length of their immature stage (6 months to 3 years) (Bouchard, 2004). Plecoptera species can be distinguished by several characteristics, but mostly by the morphology of their genitalia: epiproct and paraproct of the male and, from Nemouridae, subgenital plate of the female.

Berthélemy (1973) provided the first list of Tunisian stoneflies, including 17 species collected in valleys of Khroumiry (North-western Tunisia). Further, of the 5 *Leuctra* species recorded in the region, 4 were described as new species by Pardo & Zwick (1993) and Vinçon & Pardo (1998). *Amphinemura chiffensis* (Aubert, 1956) was recorded in Khroumiry and its nymph described for the first time (Béjaoui *et al.*, 2002–2003; Béjaoui & Boumaïza, 2004). *Protonemura algirica* (Aubert, 1956) was found by Boumaïza (2002). Additionally, two new taxa of genus *Protonemura*, *Protonemura drahamensis*

and *P. algirica bejaiana* were described by Vinçon & Pardo (2006) and Vinçon & Murányi (2009), respectively.

Four other species of genus *Protonemura* were reported from northern Africa: *P. tyrrhena* (Festa, 1938), *P. talboti* (Navás, 1929), *P. ruffoi* (Consiglio, 1961), *P. berberica* (Vinçon & Sánchez-Ortega, 1999), and *P. dakkii* Vinçon & Murányi 2009 (Aubert, 1952, 1956; Berthélemy, 1973; Gagneur & Aliane, 1991; Vinçon & Sánchez-Ortega, 1999).

The phenology of the species involves seasonal time of the life cycle's processes and synchronization of these processes. In Tunisia, the phenology of the Plecoptera species was studied for the first time by Béjaoui (2004).

During samplings in several Khroumiry mountain valleys we caught a number of specimens (adult and larvae) belonging to the new *Protonemura* species described below.

MATERIAL AND METHODS

Study area

The specimens of this species were collected in several mountain valleys located in North Western Tunisia close to Algerian border (Fig. 1). This region is the most humid in Tunisia, receiving more than 1200 mm per year of rain at an altitude ranging from 500 to 1200 m a.s.l. The streams are generally small and surrounded by dense vegetation, consisting predominantly of *Quercus faginea* and *Q. suber*. The water is cold, with low salinity and conductivity, and with high content of dissolved oxygen (Tab. 1).

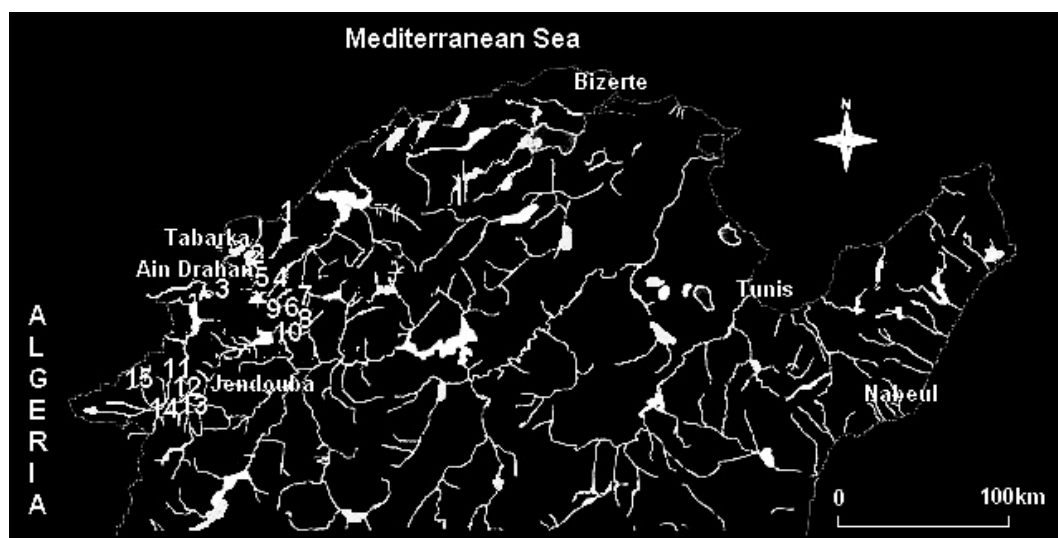


Fig. 1: Location of *Protonemura khroumiriensis* sampling sites.

Sl. 1: Lokacije vzorčnih mest za *Protonemura khroumiriensis*.

Tab. 1: Mean values of the basic physico-chemical parameters of the water: AL = altitude (m); WD = width (m); DP = depth (cm); VC = velocity current (cm s^{-1}); AT = air temperature ($^{\circ}\text{C}$); WT = water temperature ($^{\circ}\text{C}$); EC = conductivity ($\mu\text{S cm}^{-1}$ at 20°C); S = salinity (psu); DO: dissolved oxygen (mg l^{-1}); pH.

Tab. 1: Srednje vrednosti osnovnih fiziokemičnih parametrov vode: AL = nadmorska višina (m); WD = širina (m); DP = globina (cm); VC = hitrost toka (cm s^{-1}); AT = temperatura zraka ($^{\circ}\text{C}$); WT = temperatura vode ($^{\circ}\text{C}$); EC = prevodnost ($\mu\text{S cm}^{-1}$ pri 20°C); S = slanost (psu); DO = raztopljeni kisik (mg l^{-1}); pH.

Sites and its number on Fig.1	AL	WD	DP	VC	AT	WT	EC	S	DO	pH
1-Wadi Bouterfes	25	1.8	17.5	13.7	20.5	15.1	1157.9	0.3	10.5	8.03
2-Wadi Rennagha	10	1.5	17.5	17.1	19.3	16	1013	0.4	10.5	8.19
3-Wadi Ennour	400	1.5	20	16.6	17.3	16.2	528.8	0.2	11	8.25
4-Wadi Lasfar	520	4.5	12.5	26.2	17.3	12.2	176.8	0.2	10.4	6.75
5-Wadi Bransia	630	2.3	7.5	28	17.4	10.8	164.1	0.1	11.7	6.25
6-Wadi EdDmène (1)	750	0.25	12.5	13.3	15	9	130.4	0.1	11.7	6.25
7-Wadi Sardouk	625	0.35	7.5	16	17.5	9	171.1	0.1	10.6	6.25
8-Châabet Kef El Ouachi	615	1.75	12.5	12.3	17.7	11	175	0.1	10.4	6.32
9-Wadi EdDmène (2)	570	2.5	15	15.2	17.7	12.2	227	0.2	10.5	6.75
10-Châabet El Magroun (Fernana)	245	0.8	25	14.4	21.1	15.9	925.4	0.4	10	8.14
11-Wadi M'zaïef	630	0.4	12.5	12.8	17	12.2	162.7	0.1	11.3	6.75
12-Châabet El Magrouna (Aïn Soltane)	570	0.5	12.5	14.5	16.9	12.3	165.1	0.1	11.3	6.25
13-Wadi EsSoufi	230	1.2	15	11.3	18	14.3	214.3	0.2	10.1	6.75
14-Wadi Hadjar	220	1.3	15	11.2	18.9	14.5	207.9	0.2	10.1	6.25
15-Wadi Mouadjen	760	0.9	12.5	16.3	14.1	12.2	124.9	0.1	11.9	6.25

Sampling, conservation and studying methods

The adults of *P. khroumiriensis* were collected with entomological pliers placed over the stones or vegetation debris bordering the streams. The larvae were collected with the Surber net (Surber, 1937). The specimens were conserved in 70% ethanol. Description of their external morphology and illustrations of these forms were made, using a binocular stereomicroscope CARL ZEISS (0.63-6.3X), provided with a lateral drawing tube. Photographs were taken with a numerical camera, OLYMPUS (Model-C) with Zoom assembled on a binocular stereomicroscope OLYMPUS (Model SZ1145TR).

RESULTS AND DISCUSSION

Adult material studied

TUNISIA: Valley Ennour, 400m; 18-III-98: 1♂ (Holotype), 12-III-99: 9♂♂+6♀♀ (Paratypes), 8-IV-99: 3♀♀, 9-V-99: 1♀. Valley Lasfar, 520m; 18-III-98: 1♀. Valley Bransia, 630m; 18-III-98: 2♂♂+3♀♀, 8-IV-99: 5♂♂+4♀♀. Valley EdDmène, 750m; 24-III-99: 2♀♀, 6-V-99: 2♂♂+2♀♀. Valley EdDmène, 570m; 24-III-99: 1♂+6♀♀, 6-V-99: 11♂♂+19♀♀, 30-V-99: 3♀♀. Valley Sardouk, 625m; 24-III-99: 7♂♂+2♀♀, 6-V-99: 2♂♂. Châabet Kef El Ouachi, 615m; 24-III-99: 11♂♂+24♀♀, 6-V-99: 2♀♀. M'zaïef valley, 630m; 9-IV-2000: 1♂+1♀. Châabet El Magrouna, 570m; 9-IV-2000: 2♂♂+1♀. Valley Mouadjen, 760m; 9-IV-2000: 1♀. The holotype

and paratypes are deposited in the Laboratoire d'Hydrobiologie, Faculté des Sciences de Bizerte, Université 7 novembre à Carthage (Tunisia).

General diagnosis of the adults

Mean body length: male 7.1 mm, female 6.7 mm. Mean forewing length: male 9.4 mm, female 9.5 mm. General colour brown; head dark brown; legs light brown; antennae blackish with brownish spots at their insertion (Figs. 2A, B). Pronotum sub-rectangular and blackish (Fig. 3A). Gills simple without apical constriction.

Male diagnosis (Figs. 3B-F). Tergites 7, 8 and 9 slightly sclerotized, with groups of spines on central posterior margins. Tergites 8 and 9 with two median lobed expansions (resembling those of *P. ruffoi* and *P. tyrrhena*). 10th tergite with short spines around epiproct tip, visible in lateral view. Sternite 9 distally extended into a subgenital plate (hypoproct), basally with a long racket-shaped and well developed vesicle (2-2.5 longer than wider) exceeding posterior margin of 9th urite. Epiproct flattened and sarcophagus shaped in dorsal view; without small apical appendix (this is a character that distinguishes this species well from other North African *Protonemura* species). In lateral view, epiproct wide and narrowed near the tip, slightly curved upward. Ventral sclerite flat, with short spines. Paraprocts (terminology of Baumann, 1975): inner lobes hidden by the subgenital plate; median lobes with a wide basal sclerotized por-

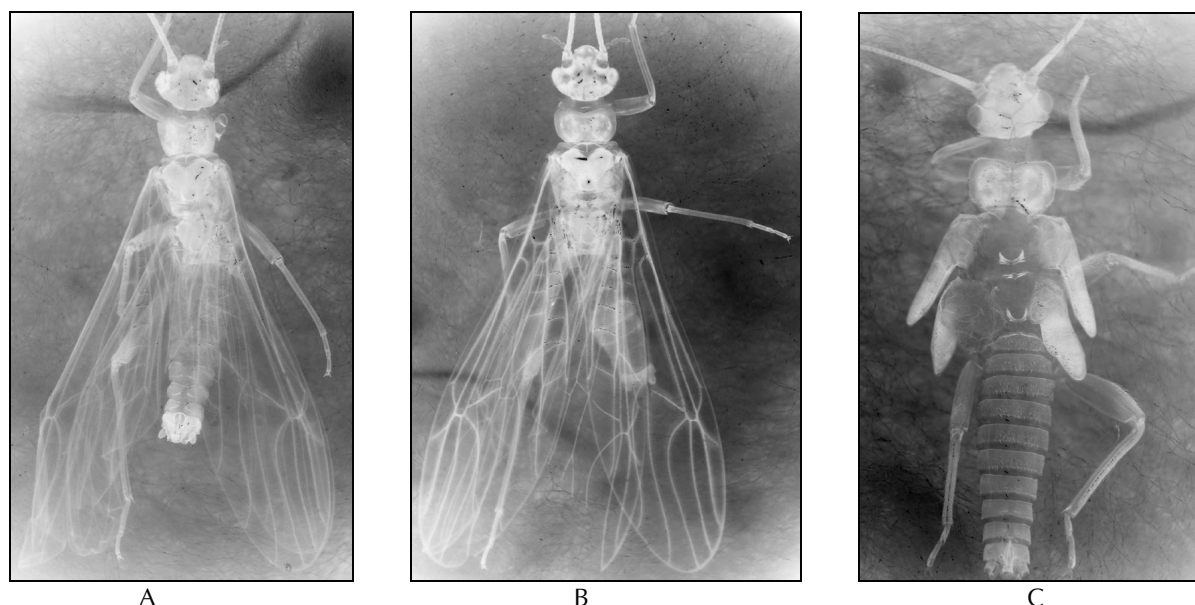


Fig. 2: *P. khroumiriensis* sp. n. Dorsal view of (A) adult male, (B) adult female and (C) mature larva.

Sl. 2: *P. khroumiriensis* sp. n. Dorzalni pogled na (A) odraslega samca, (B) odraslo samico in (C) ličinko v zreli fazi.

tion, inner darkly sclerotized branch of the median lobe curved, thick, long and sharp end, without a group of apical spines; outer lobes elongated and curved dorsally alongside cerci, ending in two spines on the external face. Cerci simple, shorter than the paraprocts.

Female diagnosis (Figs. 3G, H). 7th sternite with a median hardly pigmented pregenital plate. 8th sternite supporting a trapezoidal subgenital plate (1/2 of the sternite width), with slightly convex posterior edge. The subgenital plate well sclerotized, except in the middle area. The vaginal lobes are hidden under the subgenital plate.

Larval diagnosis. General colour brown with gloss teguments (Fig. 2C). Body length: 5.58-7 mm (male); 7.27-8.09 mm (female). Cervical gills shorter with no apical constriction. Lateral gills exposed partially in dorsal view. Setal fringe of pronotum, dense, inserted on anterolateral edge. The ratio length/width of the head equal to 0.82; the pronotum equal to 0.51 (Fig. 4A). Cerci long (35 segments), darker than the body, with short setae on the margin. 6th segment as long as wide, contrary to Algerian specimens of *P. algerica*, whose 8th or 9th segment is sub-square (Aubert, 1956), and Pyrenean specimens of *P. canigolensis* (belonging to the same group) whose 7th segment is as long as wide (Zwick & Vinçon, 1993). In the male (Fig. 4B), the form of the epiproct is similar to the adult's. The last tergite has two circular, dark and symmetrical stains. 9th tergite is furnished with two fields, with short and fine silks located near the posterior edge. In the female (Fig. 4C), 9th and 10th sternites are broader than their corresponding tergites. Under-anal lobe longer than wide, with setae to the internal edge only.

Affinities. This species is morphologically cognate to the *corsicana* group (particularly to *P. ruffoi*), which has a Circum-Mediterranean and Caucasian distribution, with several relict or insular species (Fochetti, 1994). Nevertheless, it lacks the apical appendix of the epiproct considered as an apomorphic character of *P. corsicana* group (Zwick, 1978; Fochetti, 1994). Epiproct and paraproct shapes clearly differ from other North African *Protonemura* species, particularly due to the lack of apical appendix in the epiproct tip (as pointed above). With its epiproct shape, *P. khroumiriensis* is very similar to *P. sicula* Consiglio, 1961 from Sicily (Consiglio, 1961), but this species can be easily distinguished by its different paraproct and vesicle shapes. The female is distinguished from other North African *Protonemura* species by its trapezoid subgenital plate, narrower than those of *P. algerica*, *P. talboti*, *P. berberica* and *P. tyrrhena*, and less convex than the one in *P. ruffoi*.

Ecology and phenology. *P. khroumiriensis* is a common species in the Tunisian Khroumirian valley. It has been recorded by Béjaoui (2004) at several localities between 10 and 760 m a.s.l. This species preferentially colonizes temporary streams, adapting its life cycle to the flowing period of the valleys. Although this order is known by its narrow ecological valence, the ecological profile of this species shows a clear broad ecological valence towards altitude, conductivity and the velocity current (Fig. 5). This species is the most commonly recorded, constituting 22.5% of stonefly species reported to date in the area. Its flight period lasts from late winter to late spring, but differs slightly from site to site (Fig. 6).

Etymology. This species was named after its type locality: the "Khémir" Forest of Khroumiry.

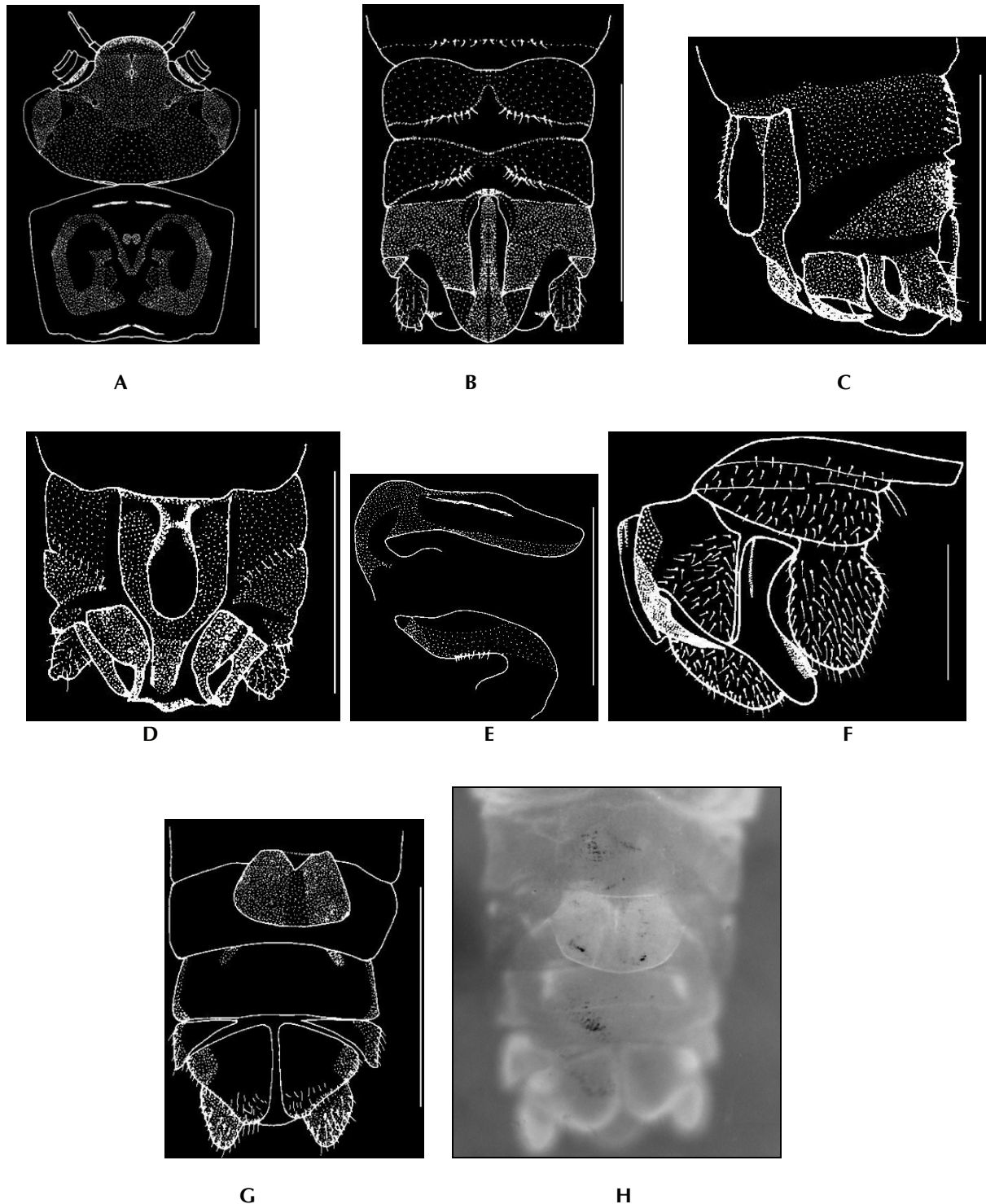


Fig. 3: *P. khroumiriensis* (adult). (A) Head and pronotum; (B) tip of male abdomen in dorsal view; (C) idem in l' lateral view; (D) idem in ventral view (0.5 mm); (E) epiproct (0.25 mm); (F) left paraproct in $\frac{3}{4}$ ventral view (0.25 mm); (G) tip of female abdomen in ventral view (0.5 mm); (H) idem (photo).

Sl. 3: *P. khroumiriensis* (odrasel primerek). (A) Glava in pronotum; (B) vrh abdomna samca, dorzalni pogled; (C) idem, l' lateralni pogled; (D) idem, ventralni pogled (0,5 mm); (E) epiprokt (0,25 mm); (F) levi paraprokt, $\frac{3}{4}$ ventralni pogled (0,25 mm); (G) vrh abdomna samice, ventralni pogled (0,5 mm); (H) idem (foto).

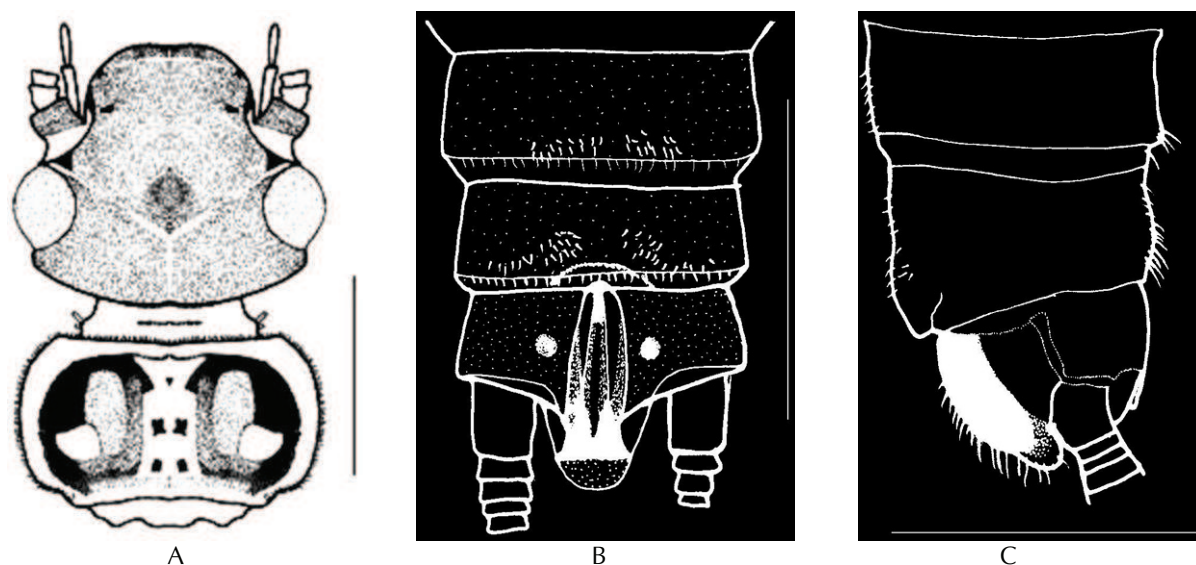


Fig. 4: *P. khroumiriensis* (larva). (A) Head and pronotum; (B) tip of male abdomen in dorsal view; (C) tip of female abdomen in ventral view (0.5mm).

Sl. 4: *P. khroumiriensis* (ličinka). (A) Glava in pronotum; (B) vrh abdomna samca, dorzalni pogled; (C) vrh abdomna samice, ventralni pogled (0,5 mm).

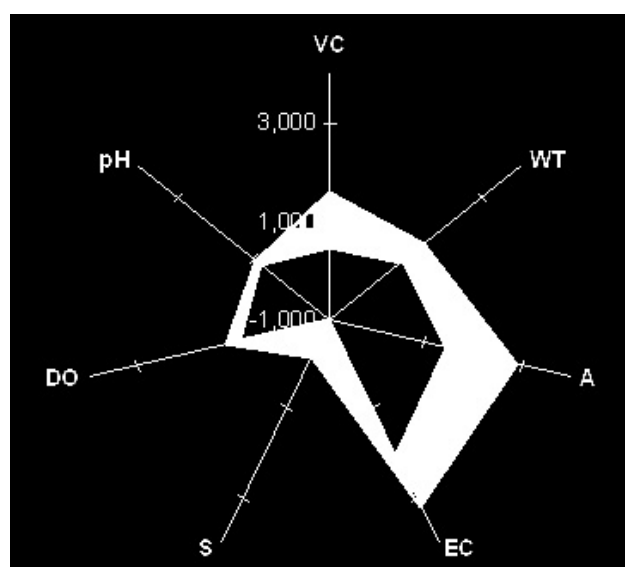


Fig. 5: Ecological profile of *P. khroumiriensis* found in Khroumirean Rivers. Legend: A = altitude (m); DO = dissolved oxygen (mg l^{-1}); EC = conductivity ($\mu\text{s cm}^{-1}$ at 20°C); S = salinity (psu); VC = velocity current (cm s^{-1}); WT = water temperature ($^\circ\text{C}$); pH.

Sl. 5: Ekološki profil vrste *P. khroumiriensis*, najdene v rekah gora Khroumirian. Legenda: A = nadmorska višina (m); DO = raztopljeni kisik (mg l^{-1}); EC = prevodnost ($\mu\text{s cm}^{-1}$ pri 20°C); S = slanost (psu); VC = hitrost toka (cm s^{-1}); WT = temperatura vode ($^\circ\text{C}$); pH.

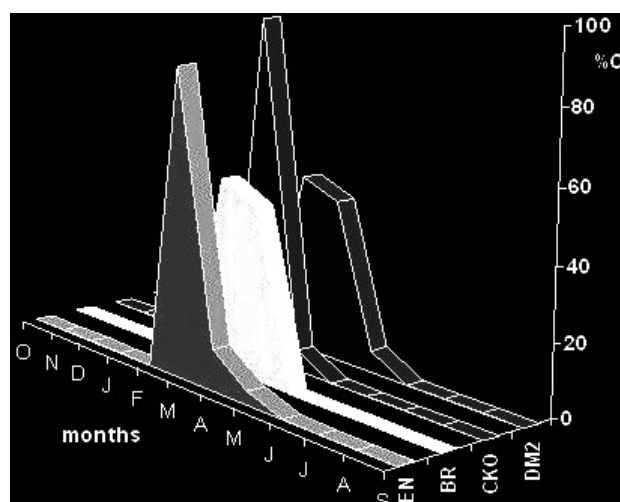


Fig. 6: Flight period of *P. khroumiriensis* from the following four streams: Ennour (EN), Bransia (BR), Châabet Kef El Ouachi (CKO) and EdDmène 2 (DM2) (%C = cumulative percentage).

Sl. 6: Obdobje letenja vrste *P. khroumiriensis* na območju štirih vodnih tokov: Ennour (EN), Bransia (BR), Châabet Kef El Ouachi (CKO) in EdDmène 2 (DM2) (%C = kumulativni odstotek).

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NOVA OPAŽANJA IN OPIS VRSTE *PROTONEMURA KHROUMIRIENSIS* SP. N. (PLECOPTERA, NEMOURIDAE) IZ TUNIZIJE

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POVZETEK

Pojav vrste *Protonemura khroumiriensis* sp.n. je bil zabeležen v številnih dolinah v tunizijskih gorah Khroumirian. Vrsta je morfološko sorodna vrsti *Protonemura ruffoi* iz skupine *Protonemura corsicana*, ki je razširjena okrog Sredozemlja in v Kavkazu. Posebej samec je zelo prepoznaven po obliki epiprokta brez apikalnega priveska in obliki paraproktov ter vezikla na 9. sternitu. Samico lahko prepoznamo po trapezoidni subgenitalni ploščici, ki je razen v sredinskem delu dobro sklerotizirana. Vrsta se naseljuje predvsem ob občasnih vodnih tokovih in svoj življenjski cikel prilagodi njihovim obdobjem pretoka. Obdobje letenja traja od pozne zime do pozne pomladi, vendar se malce razlikuje od območja do območja.

Ključne besede: Nemouridae, *Protonemura khroumiriensis*, dolina Khroumirian, Tunizija, nova vrsta

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CAVES AS POTENTIAL KARST GEOHAZARDS ON HIGHWAYS IN SW SLOVENIA

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ABSTRACT

Highways construction across the karst areas of SW Slovenia uncovered at least three times more caves than had been known prior to their construction. Sudden collapses during highways construction were documented, with some practical solutions discussed and proposed by karstologists and constructors. Beside denuded caves, many other new caves (mostly shafts) were discovered during the construction of highways in SW Slovenia. We have only few documented examples of sudden collapses along highways that have been opened to traffic for almost 40 years. In this sense, the highways in SW Slovenia are stable and have posed no great risk for karst geohazards so far. However, regular monitoring of highway stability, especially in supposed weaker places (remediated shafts directly under highway), is recommended.

Key words: highway construction, cave, karst, geohazard, Slovenia

GROTTE QUALI POTENZIALI GEO-PERICOLI PER LE AUTOSTRADE DELLA SLOVENIA SUD-OccIDENTALE

SINTESI

Con la costruzione di autostrade nell'area carsica della Slovenia sud-occidentale il numero di grotte scoperte si è almeno triplicato. Improvvisi collassi avvenuti durante la costruzione sono stati documentati ed alcune soluzioni pratiche sono state applicate da carsologi e costruttori. Durante la costruzione di autostrade nella Slovenia sud-occidentale sono stati ritrovati, oltre alle grotte denudate, anche altri tipi di grotte, soprattutto a strapiombo. Visto che il numero dei casi di collassi improvvisi di autostrade (in uso da quasi 40 anni) è minimo, gli autori concludono che le autostrade della Slovenia sud-occidentale sono stabili e sicure e non rappresentano grandi rischi per i geo-pericoli carsici. In ogni caso è consigliabile che la stabilità delle autostrade venga monitorata regolarmente, soprattutto nelle aree instabili, quali pozzi risanati sottostanti le autostrade.

Parole chiave: costruzione autostrade, grotte, carso, geo-pericolo, Slovenia

INTRODUCTION

Few decades of highway construction in the Slovene karst areas is useful not only for a better traffic solution, but for new scientific data on karstology and speleology as well. Besides technical solutions for applied karst problems in highway construction, a big step in theoretical approach in karst geomorphology was also made. Many denuded caves were discovered (Fig. 1) representing old horizontal cave passages filled with cave sediments (Knez & Šebela, 1994; Mihevc, 1996; Mihevc *et al.*, 1998; Šebela, 1999; Mihevc, 2001; Knez & Slabe, 2002). Due to the processes of tectonic uplifting, erosion and corrosion, they have lost their roofs. In the past, such karst features were described as dolines or karst depressions filled with remains of old surface stream sediments. But many dolines are in fact remains of old denuded caves. One third of all dolines in Slovene Kras are supposed to be remains of old caves (Mihevc, 2001).

A horizontal karst depression filled with sandstone pebbles and cave sediments that were discovered during the construction of Divača–Dane highway was the first denuded cave studied in detail (Knez & Šebela, 1994; Šebela & Mihevc, 1995; Mihevc, 1996, 2001). Flowstone depositions on original cave passage wall and over cave sediments proved that this was an old karst cave, and not a surface stream valley.

Besides denuded caves, many new caves were opened during the highway construction in SW Slovenia. Since 1994, more than 350 new caves have been discovered in the course of building some 60 km of new highways (Knez *et al.*, 2008; Knez & Slabe, 2009). Some of them opened as collapses during the construction. In this sense, the question about caves as possible karst geohazards on Slovene highways was unveiled. A geohazard can be defined as a geological state that represents or has the potential to develop further into a situation leading to damage or uncontrolled risk (<http://en.wikipedia.org/wiki/Geohazard>).

In the Slovene karst areas generally, not only on highways, there are some examples of collapses, but not as many as on gypsum karst (Cooper, 1995; Fuleihan *et al.*, 1997) or karst areas where ground-water pumping is causing sudden subsidences, such as in southern and southeastern USA (Leake, 2004). Gospodarič (1962) described a sudden sinkhole collapse at Tomaj in Kras, which caused destruction of the house as it was founded on karst cavity filled by the sediments. Frequent are the collapses due to human interventions on the karst surface. While blasting the cess-pool for a house at Kozina, 2 m thick roof of a big underground chamber (Habič, 1984) suddenly collapsed. During the road construction between Divača and Koper, three major potholes appeared. The deepest pothole was 50 m deep. Huge caves were met at the construction of the road near Sežana (Habič, 1984).



Fig. 1: Denuded cave with partly removed sediments on Divača–Kozina highway, August 1997. (Photo: S. Šebela)

Sl. 1: Denudirana jama z delno odstranjenimi sedimenti na avtocesti Divača–Kozina, avgust 1997. (Foto: S. Šebela)

While building about 500 km of highways (1991–2008) in the Croatian karst region, over 945 caverns were discovered. Most of them (85.5%) are vertical speleological structures, while 14.5% are horizontal speleological structures. The deepest cave reaches -196 m, whereas the longest cave is known to have 1,490 m of passages (cavern in the Učka tunnel). "Kaverna u tunelu Sveti Rok" was discovered in the left-side Sveti Rok tunnel, and has 1,137 m of channels. The cave was subjected to speleological investigations and topographic surveys. The preparation of cavern remediation design solutions was greatly facilitated by speleological investigations. At some points, the roadway route had to be partly modified, but the groundwater flow patterns, discovered during speleological investigations, have in no case been altered (Garašić, 2009). In November 2004, an access to a very big cave (almost 4 km long and about 220 m deep)

named "Grotta Impossibile" was found near Trieste (Catinara) in Italy during tunnel construction (Torelli & Guidi, 2006). The cave is preserved and tunnel construction works considered all safety requirements.

Highway construction across karst areas in SW Slovenia as well as in Croatia and Italy opened many new unknown caves. When the upper part of the karst surface (1–10 m) is removed, epikarst shows its uppermost characteristics with significant increase of entrances to unknown caves. In this paper, selected caves situated below highways in SW Slovenia are presented as potential karst geohazards. There are only few examples of sudden collapses along highways when they have already been used for traffic. In this sense, highways in SW Slovenia are very stable so far.

The study was performed as part of the projects sponsored by DARS d.d. (Motorway Company in the Republic of Slovenia) and DDC svetovanje inženiring d.o.o. (DDC Consulting & Engineering Ltd.) and as collaboration with The Institute of the Republic of Slovenia for Nature Conservation, regional unit Nova Gorica and the Ministry of the Environment and Spatial Planning.

METHODS

To understand caves as potential karst geohazards, detailed topographic maps of previously known and newly discovered caves are necessary, as well as determination of the precise position of cave entrances regarding the highway lines. Some karstologic and geomorphologic research had been carried out prior to highway construction and during the construction itself. In this sense, the idea of what could be found some meters below the karst surface before and during the construction became clearer. The fact is that highway construction across the karst areas of SW Slovenia uncovered at least three times more caves as known before the construction (example from the Divača–Kozina highway). Sudden collapses during highway construction were documented and some practical solutions discussed between karstologists and constructors. For constructors the main objectives are safe and stable mechanical properties of highways. Karstologists are looking to protect caves and other karst features as much as possible. In such a manner, technical solutions suitable for both partners were realized (Knez *et al.*, 2008).

In the event of new cavities being discovered during highway construction, drilling has to determine hazards for eventual collapses. Here, georadar research (Knez & Slabe, 2005a) can be an important method for identification of road subsidence.

RESULTS AND DISCUSSION

In SW Slovenia, there are some roads (Divača–Koper) and highways (Vrhnika–Postojna) that have been

opened to traffic for few decades. Even though used for 30 or 50 years, only few collapses have been reported. The roads across the karst in SW Slovenia are in fact very stable. More collapses occur during highway construction, when mostly associated with blasting of strongly karstified areas. In this way, many new unknown caves have been discovered. But with correct remediation decisions, the problems are solved and so far the new highways across the karst in SW Slovenia show very good stability.

Vrhnika–Postojna highway section

During the highway construction between Vrhnika and Postojna, 22 cavities (7 cavities/km² on average) without natural entrances were discovered (Kranjc, 1983). The area is built of limestone, dolomite and dolomitic breccia. While building the three viaducts on the Vrhnika–Postojna highway, the planner had to change the projects and replace the foundations due to the fact that karst caves were situated just below (Habič, 1984).

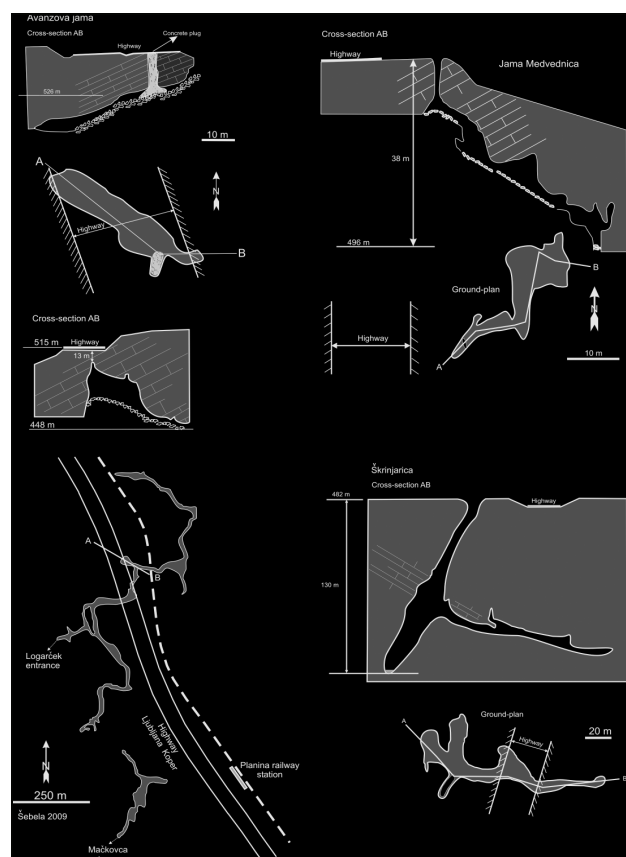


Fig. 2: Position of some caves situated below or near highways.

Sl. 2: Položaj nekaterih jam, ki ležijo pod avtocestami ali v njihovi bližini.

Near Postojna, at the contact of limestone and non-carbonate rocks, not all the debris that partly filled up the karst cave was removed during the highway construction. This fact later caused the subsidence of the roadway. After a decade, the road was in need of repair as a part of the roadway collapsed. In 1993, twenty-one years after the road was completed, the cavity of about 10 m³ occurred at Verd near Vrhnika. The cave entrance opened in-between two highway lines due to the lower layer of gravel falling into the unfilled cave below.

Directly under the Vrhnika–Postojna highway (29 km long, constructed in 1972), some very deep shafts were included in the highway construction. Many shafts are no longer accessible, as the highway runs over them ("Brezno II pod železniško postajo Planina" (13 m deep), Avanzova Jama (28 m deep), Škantlovo Brezno (10 m deep)). The cave passage of Avanzova Jama is situated directly under the highway (Fig. 2). The cave is 47 m long and 28 m deep. Roof thickness between the cave passage and the highway ranges from 10 to 20 m. During the construction, the original entrance shaft was filled with material and covered with concrete plug. The entrance to Jama Medvednica (Fig. 2) is situated only some meters to the east from the Vrhnika–Postojna highway.

Just under the Vrhnika–Postojna highway and the railroad near Planina railway station, the 2,285 m long and 83 m deep karst cave Logarček is situated (Gams, 1963) (Fig. 2). One of its collapse chambers called Podorna Dvorana is directly under the eastern edge of the highway (Fig. 2). The roof thickness between the cave and the surface is 13 m. The Logarček cave is often affected by high waters. Part of the cave can sometimes be flooded and inaccessible. The Podorna Dvorana, however, is never affected by high floods. Cavers claim that sounds of highway and railway traffic can be heard in the cave. But we do not have any solid evidence that some collapse blocks in the Podorna Dvorana have fallen down due to highway traffic.

Dane–Fernetiči highway section

Two tunnels (240 and 260 m long) were constructed in the 4.8 km long Dane–Fernetiči highway (Fig. 3). Just at the exit of the southern tunnel, a bigger (5x10 m) cave opened with collapse due to blasting. The cave was filled with block material and protected by concrete plate. Just between both tunnels, two vertical shafts of up to 30 m deep were discovered. One of them had been formed along a well-expressed fault (Fig. 3).

Near the highway, a 109 m deep shaft was discovered. The entrance to the cave was in a doline, which is used as catchment area for waste waters from the highway. Special arrangements for the protection against leakage into the cave were carried out (Slabe, 1997a).

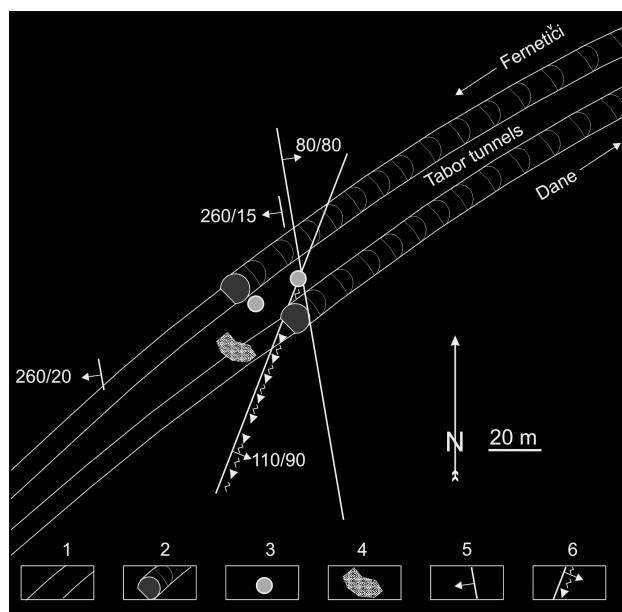


Fig. 3: Tabor tunnel. Legend: 1 = highway; 2 = Tabor tunnel; 3 = shaft opened during highway construction; 4 = cave opened during highway construction; 5 = strike and dip direction of bedding-planes; 6 = strike and dip direction of fault zone.

Sl. 3: Predor Tabor. Legenda: 1 = avtocesta; 2 = predor Tabor; 3 = brezno, odprto med graditvijo avtoceste; 4 = jama, odprta med graditvijo avtoceste; 5 = smer vpada in vpadni kot plasti; 6 = smer vpada in vpadni kot prelomne cone.

Divača–Kozina highway section

With preliminary karstologic and geologic field studies on the 6.7 km long planned highway, 4 denuded caves were determined (Šebela, 1996). This was the proof that denuded or roofless caves can be determined primarily from original morphological shape of depressions and dolines. During highway construction, 2 more denuded caves were opened by construction works.

Besides denuded caves, other unknown smaller or bigger caves were also detected during preliminary studies. On the 6.7 km long highway, 9 new caves were found apart from the 6 already known caves (Kataster jam IZRK ZRC SAZU). This means that with the preliminary karst studies carried out before highway construction, 2.2 caves per 1 km of the road were determined (Šebela, 1996, 2000).

Later on, during the Divača–Kozina highway construction, 50 caves were discovered along the 7.5 km long highway (Slabe, 1998) or 6.6 caves per 1 km, which is three times more than during the preliminary karstologic studies. The entrance to Jama nad Škrinjaričo (Fig. 2) is situated 35 m W from the Divača–Kozina highway (Šebela, 1996). The cave is 270 m long and

130 m deep. The thickness of the cave roof under the highway is 85 m. The highway over Jama nad Škrinjaričico has been opened to traffic since 1997. The cave has developed in limestones of Liburnian formation (K, Pc). The entrance is situated at 482 m. The horizontal passage has rich flowstone decorations and many old Italian inscriptions. The cave map has already been published in the book "Il Timavo" (Boegan, 1938).

Between Škocjanske Jame and Kačna Jama, there is an unknown passage of the river Reka, which runs about 200 m beneath the highway, which means that the thickness of carbonate rocks between the cave and the surface is about 150 m. During the excavation works carried out on the Divača–Kozina highway, small entrances to shafts were discovered in the base of dolines. These entrances were covered by large blocks and further reinforced by concrete. Next, a layer of rubble was spread on top and consolidated by a vibration roller. The depth of the deepest shaft that was treated in such a manner was 51 m (Slabe, 1997b).

The Kastelec tunnel

In order to estimate the degree of karstification for the planned Kastelec tunnel, preliminary karstologic and geologic studies were performed. Within the studied area, only two caves (Brezno na Škrklovici and Udor na Škrklovici) had been known from cave register (Kataster jam IZRK ZRC SAZU). The position of Brezno na Škrklovici was precisely determined. The entrance shaft that is about 10 m deep has developed within Dinaric (NW–SE) and cross-Dinaric (SW–NE) oriented fissures. Alveolinid-nummulitid Eocene limestone dips towards SE for 20°, i.e. in the same direction as the cave passage. The cave is 200 m long and 115 m deep.

In the cave Udor na Škrklovici, two fissure sets prevail, one is of E–W, the another of Dinaric (NW–SE) orientation. The cave has two entrances. One is from collapse doline, while the other represents some 8 m deep shaft. The cave is 35 m long and 10 m deep. Thick-bedded Alveolinid-nummulitid Eocene limestone dips towards NW for 10°. Between Brezno na Škrklovici and Udor na Škrklovici, bedding-planes are folded into a gentle anticline, as shown on the cross-section in Figure 4.

During the excavation of the NE entrance to the Kastelec tunnel, some unroofed caves were discovered (Knez & Slabe, 2002, 2005b). The biggest cave had a diameter of 18 x 9 m and was filled with cave sediments (Fig. 5). Individual portions of the caves, which were unroofed and resembled dolines, were clearly evident on the surface before the construction work began. During the excavation of the Kastelec tunnel, the largest cave complex (LC-S647) was discovered in the tunnel near the cave Brezno na Škrklovici (Fig. 4). In the tunnel, three

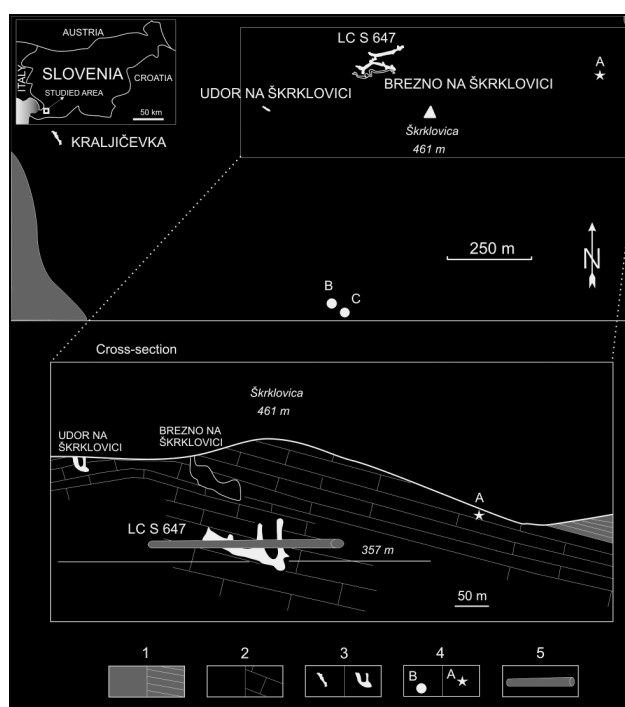


Fig. 4: Kastelec tunnel. Cross-section height is 3-times enlarged. Legend: 1 = Eocene flysch; 2 = Eocene alveolinid-nummulitid limestone; 3 = cave ground-plan and cave cross-section; 4-black point = rock shelter: B-Podmol, C-Acijev spodmol; 4-black star = position (A) of an old cave filled with sediments in Figure 5; 5 = Kastelec tunnel.

Sl. 4: Predor Kastelec. Višina prečnega profila je 3x povišana. Legenda: 1 = eocenski fliš; 2 = eocenski alveolino-numulitni apnenec; 3 = tloris jame in prečni profil jame; 4-črna pika = spodmol: B-Podmol, C-Acijev spodmol; 4-črna zvezda = položaj (A) stare jame, zapolnjene s sedimenti na Sliki 5; 5 = predor Kastelec.

major passages that were not interconnected were discovered, but in speleogenetical view they are part of the same cave complex. The dip angle of the limestone layers is 30–40° towards the west. The cave passages follow, in general, the dip of the layer with a declination of 15°. More powerful tectonic zones have Dinaric and cross-Dinaric orientations and an almost north-south orientation. Collapsed zones predominate. Chimneys in the cave, which reach up to 40 m in height, usually follow the tectonic zones.

All four caves (Brezno na Škrklovici, Udor na Škrklovici, the cave in the left pipe of the Kastelec tunnel LC-S647, and the old cave filled with sediments at the NE entrance to the Kastelec tunnel in Figure 5) formed in Eocene Alveolinid-nummulitic limestone. Although Brezno na Škrklovici and the cave in the left pipe of the Kastelec tunnel LC-S647 are no longer connected,



Fig. 5: Cave filled with sediments at NE entrance to the Kastelec tunnel. (Photo: S. Šebela)

Sl. 5: Jama, zapolnjena s sedimenti na SV strani vhoda v predor Kastelec. (Foto: S. Šebela)



Fig. 6: Doline remediation on Divača–Kozina highway, early spring 1995. (Photo: S. Šebela)

Sl. 6: Sanacija vrtače na avtocesti Divača–Kozina, zgodnja pomlad 1995. (Foto: S. Šebela)

speleogenetically they are part of the same cave system. Different passages of the cave system LC-S647 are today accessible through concrete pipes and door entrance accessible from the Kastelec tunnel (Knez & Slabe, 2009).

CONCLUSIONS

Highways in SW Slovenia run over the well developed karst. There are no bigger building problems because the rock is solid enough and not covered by thick sediments. Some problems during the construction are connected with karst depressions and caves, which are filled by the sediments having poor mechanical properties (Knez & Slabe, 2007). They may be detected by preliminary karstologic and geologic research prior to road construction, but most of them are discovered during the earthworks only.



Fig. 7: Unknown cave opened on Divača–Kozina highway, early spring 1995. (Photo: S. Šebela)

Sl. 7: Neznana jama, ki se je odprla na avtocesti Divača–Kozina, zgodnja pomlad 1995. (Foto: S. Šebela)

The karst features within the road construction must be suitably treated. From the dolines and the caves all sediments are removed and the bottom is filled by carbonate rubble, later grouted by the concrete (Fig. 6). The experience acquired during previous highway constructions, when the treatment was similar, indicate good results.

Almost 40 years of experience with studies of karst surface and underground features across SW Slovenia are showing good mechanical stability of highways (Kranjc, 1983; Kranjc *et al.*, 1991; Knez *et al.*, 2008). Some collapses occurred near or between highway lines. On the other hand, on highways, which are still under construction, collapses (Fig. 7) occur even during the last consolidation of gravel roadway by vibration rollers.

On our highways, we have just some examples of cave or doline collapses in the period when a highway has been opened to traffic for several years. Most causes are due to mistakes in construction or owing to incorrect wash out of sediments along highways. The Karst Research Institute ZRC SAZU makes detailed cave maps with special regard to thickness of cave roof and stability of newly opened caves. So far, the good stability on Slovene highways is probably also connected with the fact that the karst of SW Slovenia is not covered with thicker sediments or soil. However, regular monitoring of highway stability, especially at supposed weaker places (remediated shafts directly under highway), is recommended.

JAME KOT MOŽNE KRAŠKE GEO-NEVARNOSTI NA AVTOCESTAH V JZ SLOVENIJI

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POVZETEK

Med graditvijo avtocest čez kraške terene JZ Slovenije je bilo odkritih veliko novih neznanih jam. Ko je zgornji del (1–10 m) kraškega površja odstranjen, se pokažejo značilnosti zgornjega dela epikrasa in močno naraste število vhodov v neznane jame. V tem članku so obravnavane izbrane kraške jame pod avtocestami v JZ Sloveniji kot možne kraške geo-nevarnosti. Zabeleženih je le nekaj primerov nenadnih udorov vzdolž avtocest, ko so bile te že odprte za promet. Avtoceste v JZ Sloveniji so v tem smislu za zdaj stabilne.

Da bi razumeli jame kot možne kraške geo-nevarnosti, je treba izdelati natančne topografske karte predhodno znanih jam in novih jam, prav tako pa moramo natančno določiti jamske vhode glede na traso avtoceste. Nekaj krasoslovnih in geomorfoloških raziskav je bilo opravljenih pred graditvijo avtocest in med samo konstrukcijo. Dejstvo je, da je graditev avtocest v JZ Sloveniji odkrila najmanj trikrat več jam, kot jih je bilo znanih pred konstrukcijo (primer avtoceste Divača–Kozina). Nenadni udori med graditvijo avtocest so bili dokumentirani in nekatere praktične rešitve so bile predmet razprave in rešitve med krasoslovci in gradbeniki. Za gradbenike sta pomembni stabilnost in varnost avtocest, za krasoslovce pa je pomembno čim bolj ohraniti jame in druge kraške pojave.

Skoraj 40-letne izkušnje krasoslovnega spremljanja graditve avtocest čez kras v JZ Sloveniji kažejo dobro mehaniko stabilnost avtocest. Večina udorov ali jam se je odprla ob ali med voznima pasovoma. Po drugi strani pa na avtocestah, ki še niso končane, udori nastajajo še po zadnjih utrjevanjih cestišča z vibracijskimi teptalnimi stroji.

Dobra stabilnost slovenskih avtocest je verjetno povezana tudi z dejstvom, da kras JZ Slovenije ni na debelo pokrit s sedimenti ali prstjo. Kljub vsemu pa je priporočljivo redno spremljanje stabilnosti avtocest, posebno na domnevno nestabilnih mestih, kot so sanirana brezna neposredno pod avtocesto.

Ključne besede: graditev avtoceste, jama, kras, geo-nevarnost, Slovenija

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DELO NAŠIH ZAVODOV IN DRUŠTEV

ATTIVITÀ DEI NOSTRI ISTITUTI E DELLE NOSTRE SOCIETÀ

ACTIVITIES BY OUR INSTITUTIONS AND ASSOCIATIONS

**DELO NAŠIH ZAVODOV IN DRUŠTEV
ATTIVITÀ DEI NOSTRI ISTITUTI E DELLE
NOSTRE SOCIETÀ
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**SAME11 (Symposium on Aquatic Microbial Ecology) –
11. Simpozij mikrobne ekologije voda**

Morska biološka postaja Nacionalnega inštituta za biologijo je v letošnjem letu organizirala mednarodni simpozij o mikrobni ekologiji voda SAME11 (*Symposium on Aquatic Microbial Ecology*), ki je potekal od 30. avgusta do 4. septembra 2009 v hotelu Bernardin v Piranu. Srečanje je potekalo pod pokroviteljstvom predsednika države dr. Danila Türka. V pozdravni besedi se je simpozij poklonil jubileju Charlesa Darwina, kajti njegovi dokazi in razmišljanja o razvoju vrst in selekciji organizmov v evoluciji bolj kot kdajkoli prej zaposlujejo ne le evolucijske biologe, pač pa tudi mikrobiologe.

Simpozij o mikrobni ekologiji voda je z aktivnostjo formalno začel po letu 1982, ko sta se združila takratna simpozija International Workshop on the Measurement of Microbial Activities in the Carbon Cycle of Aquatic Environments in European Marine Microbial Symposium (EMMS). Po letu 1999 poteka simpozij redno vsako drugo leto. Pred štirimi leti, na srečanju na Univerzi v Helsinkih na Finskem, je Morska biološka postaja predlagala Mednarodnemu organizacijskemu odboru SAME9 organizacijo srečanja v Sloveniji. Kandidatura je bila potrjena na naslednjem zasedanju mednarodnega odbora v Faru na Portugalskem leta 2007. Letošnje srečanje je potekalo pet dni, udeležili pa so se ga mikrobiologi, virologiji, molekularni biologi, biokemiki, informatiki in modelisti, raziskovalci, ki se ukvarjajo z mikrobi v vodah, atmosferi in sedimentih. Tematika vključuje različne ekosisteme, od globokomorskih do obalnih, estuarijev, rek in jezer, vse od polarnega do tropskega geografskega pasu. Program je vključeval devet trenutno najbolj aktualnih tematik: Biodiverziteti v mikrobni ekologiji, Mikrobi in biokemični cikli, Transformacija organske snovi v vodnih sistemih, Mikrobne interakcije in komunikacija, Ekologija virusov, Mikrobiologija sedimentov, Mikrobi in klimatske spremembe ter Modeli v mikrobni ekologiji. Sodelovalo je več kot 200 raziskovalcev iz 30 držav, najštevilčnejša pa je bila udeležba iz Nemčije, Španije, Švedske in Slovenije. Poleg predstavnikov večine evropskih držav so bili prisotni tudi raziskovalci iz ZDA, Kanade, Nove Zelandije, Japonske, Tunizije in Brazilije. Rezultati so bili predstavljeni v 90 ustnih predavanjih in 100 posterjih, povzetki pa zbrani v tiskani in elektronski obliki.

Danes vemo, da so mikroorganizmi najštevilčnejši prebivalci planeta in imajo pomembno vlogo v vseh

ekosistemih. Ker so zelo prilagodljivi in se hitro razmnožujejo, vplivajo na biogeokemične cikle in kroženje posameznih elementov v naravi ter zagotavljajo hranila vsem drugim organizmom. V uvodnem predavanju je profesor Farooq Azam (Scripps Inštitut za oceanografijo, San Diego, ZDA) poudaril, da oceani prekrivajo 75% celotne zemeljske površine in da je vpliv mikroorganizmov na spremembe klimatskih razmer večji, kot smo predvidevali. Opozoril je na vse bolj prisotno spoznanje o povezanosti zdravja oceanov in zdravja ljudi. Oceani so vektorji za prenos mikroorganizmov, med drugim tudi patogenih bakterij, ki ogrožajo zdravje človeka, kot je primer *Vibrio cholerae*. Globalna otoplitev in z njo povezan dvig morske gladine utegneta močno povečati število obolenj s kolero kot tudi drugimi nevarnimi boleznimi. Da bi to bolje obvladovali in oblikovali primerno strategijo ukrepov, bi morali bolje razumeti biologijo, biokemijo mikrobov od nano-metrskih do oceanskih razsežnosti.

O posledicah globalnih podnebnih sprememb na okolje je v uvodni besedi sekcije Mikrobi in klimatske spremembe opozarjal tudi dr. Jean-Pierre Gattuso iz Oceanografskega observatorija v Villefranche-sur-mer v Franciji. Opozoril je na problem povečanih koncentracij ogljikovega dioksida in zakisanja morij in oceanov kot posledici globalne otoplitve. Določene spremembe se kažejo v celični zgradbi, bioloških in fizioloških lastnosti nekaterih mikroorganizmov, povečani toksičnosti ali vrstni sestavi in razporeditvi združb v nekaterih posebej ranljivih področjih, kot so npr. ledeniki.

Sicer pa je bilo največ prispevkov predstavljenih v sekcijah Mikrobi in biokemični cikli ter Transformacija organske snovi v vodnih sistemih. Predstavljeni so bili rezultati vloge heterotrofnih dušičnih fiksacijskih bakterij v Baltiku, kompeticijski procesi značilni za fosforno limitativna okolja, kot je Mediteran, vloga arhej v globokomorskih in sladkovodnih sistemih, genomske analize, fiziologija in ekologija bakterij v oksidnih/anoksidnih conah. Zanimanje je vzbudilo tudi predavanje o glivah v območjih z veliko vsebnostjo soli, kot so Sečoveljske soline. Še vedno so aktualne razprave o procesih gibanja mikroorganizmov, tvorbi ali razgradnji biofilmov, mikro in makroagregatov ali morske sluzi.

Predstavljeni so bili rezultati novih tehnik določanja vrstne sestave mikroorganizmov in merjenja hitrosti rasti posameznih dominantnih skupin. Pri raziskavah mikroorganizmov voda se namreč vedno srečujemo s problemom izolacije posamezne skupine organizmov ali posamezne celice v množici raznovrstnih organizmov, ki istočasno naseljujejo naravna vodna okolja. Vplive sprememb poskušamo dandanes razumeti na samem nivoju celic in genov, za kar so potrebne nove molekularne in optične tehnike. Rezultati določanja vrst s pomočjo novih tehnologij (npr. 454 pirosekvenciranje) kažejo, da je v morjih in oceanih prisotnih še več vrst bakterij in arhej, kot smo predvidevali, njihova vloga pa je v veliki

meri neznana. Nekatere vrste so prisotne v velikem številu in nastopajo v zelo različnih ekosistemi, obratno so nekatere redke in maloštevilne. Glede na množico podatkov genetskih sekvenc je potrebna previdna interpretacija in evalvacija rezultatov.

Tehnologija molekularnega raziskovanja postaja dosegljiva tudi področju raziskav bakterijske simbioze, s katerim se ukvarja laboratorij prof. Mc Fall-Ngaive z ameriške univerze Wisconsin Madison. Večina simbioz temelji na prehranski vzajemnosti gostitelja in gosta. Sama že vrsto let proučuje dnevno-nočni ritem simbioze med havajsko sipo (*Euprymna scolopes*) in luminescenčnimi bakterijami *Vibrio fischeri*. Pri raziskavah so na podlagi številnih izoliranih genov gostitelja in bakterij ugotovili, da je pomembna sinteza in delovanje določenih encimov. Oba organizma imata genetsko določene procese, ki potekajo v 24 urah medsebojnega sožitja, pri tem pa imata oba koristi; s tem je povezano tudi vedenje obeh organizmov. Glede na to, da devet desetlin vseh človeških celic predstavljajo bakterije in je znanih več kot 2000 vrst le-teh, so oblike interakcij mikrobov, njihova vloga in procesi simbioze pomembni. Šele z novimi tehnikami molekularne biologije, ki so nam na voljo v zadnjih letih, odkrivamo njihovo vlogo. Tovrstne raziskave nam dajejo odgovore na vprašanja, zakaj so nekatere bakterije koristne ali škodljive, kakšen je njihov odnos z rastlinami ali živalmi, tudi človekom. Pomembno je, v kakšnem molekularnem jeziku bakterije komunicirajo z nami in okoljem na ravni genov.

Podobno je tudi v zaključnem govoru povzel prof. Gerhard Herndl z Univerze na Dunaju, ko je dejal, da so nujno potrebne raziskave, usmerjene v proučevanje vzajemnih odnosov mikrobov z okoljem in to predvsem na celičnem nivoju. Filogenetsko in funkcionalno raznovrstnost mikrobne združbe bolje razumemo s pomočjo rezultatov novih tehnik, kot so (meta)genomika, (meta)transkriptomika in proteomika. Vprašanje pa je, če ekologijo mikrobov v vodah in njihovo vlogo v biogeokemičnih ciklih lahko razumemo brez poznavanja aktivnosti posamezne celice v mikrookolju.

Ob koncu simpozija bo objavljena posebna številka priznane mednarodne revije Aquatic Microbial Ecology SAME11 (izdajatelj: Inter-Research), kjer bodo zbrani pregledni članki vseh uvodnih predavanj simpozija. Simpozij so s finančno podporo omogočili Javna agencija za raziskovalno dejavnost Republike Slovenije, Evropska znanstvena fundacija, Nacionalna komisija UNESCO/IOC, Splošna plovba d.o.o., Komunalno podjetje Domžale ter Občina Piran in Mestna občina Koper. Vsa gradiva (znak, zloženko in knjigo abstraktov) je oblikoval akademski slikar Tilén Žbona.

Simpozij je ob svoji 40-letnici organizirala Morska biološka postaja, enota Nacionalnega inštituta za biologijo. Od začetka njenega delovanja je bila v raziskovalne in aplikativne dejavnosti aktivno vključena tudi skupina mikrobiologov. V otvoritvenih govorih je bil podan kratek pregled delovanja Morske biološke postaje in predstavljen njen pomen v lokalnem prostoru. Dolgoletna sodelovanja sodelavcev Morske biološke postaje z uglednimi raziskovalci iz tujine so omogočila organizacijo izjemno kvalitetnega simpozija in s tem dodatno ucvrstile mednarodni ugled edine slovenske morske raziskovalne institucije ter nedvomno uvrstile Slovenijo na zemljevid obmorskih držav, ki se z morjem uspešno ukvarjajo tudi na raziskovalnem področju.

Vode so življenjsko pomemben ekosistem in ohranjanje njihovega ravnovesja je odvisno od pravilnega razumevanja procesov in s tem pravilnih odločitev. Še vedno smo daleč od tega, da bi razumeli vlogo mikrobov v ekologiji, zato so poleg objav rezultatov potrebna tudi medsebojna srečanja, spoznavanja in izmenjava znanja med raziskovalci, predvsem pa med raziskovalci in študenti, kar je osnovni namen simpozija. Naslednje srečanje, SAME12, bo organiziral Leibnitz inštitut za raziskave Baltika, potekal pa bo v Warnemündeju v Nemčiji.

Valentina Turk



Avtor: T. Žbona

ANNALES

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PROJECT MEDUZA IN THE CONTEXT OF ITS HISTORICAL TIME

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ABSTRACT

In 2001, the National Science Foundation, in union with the Croatian and Slovenian science ministries, provided initial support for the international collaboration that has become the Meduza project. The program was started with the goal of international collaboration. The scientists involved in the project were glad to oblige because we wanted to work together. Our initial objective was simple – use this international collaboration to develop exciting scientific research involving medusae in Southern Adriatic waters. During the subsequent eight years we collaborated on six joint summer research trips. This international collaboration has been of great importance personally and professionally to all of the investigators and institutions involved in the project, but we now ask what objective difference has the project made scientifically? We approach that question by comparing what we thought we might accomplish at the project's outset to how we now view research on gelatinous zooplankton because of research in the Meduza project. Work outside the program also has affected our views but we describe here research produced through the project that has contributed substantially to broadening our perspectives in three major areas of investigation: modes of propulsion, mechanics of predation, and trophic significance of medusae.

Key words: Meduza project, propulsion, distribution, hydrodynamics, foraging, trophic roles

PROGETTO MEDUZA NEL CONTESTO DEL SUO SVILUPPO STORICO

SINTESI

La Fondazione Nazionale di Scienze (National Science Foundation) degli USA ed i Ministeri per la Scienza croato e sloveno hanno approvato, nel 2001, la collaborazione internazionale che ha poi portato al progetto Meduza. Il programma è stato avviato allo scopo di sviluppare la collaborazione internazionale. Gli scienziati coinvolti nel progetto hanno accolto positivamente l'obbligo, in quanto desiderosi di lavorare assieme. L'obiettivo iniziale era semplice – usare la collaborazione internazionale per sviluppare la ricerca scientifica incentrata sulle meduse dell'Adriatico meridionale. Durante gli otto anni successivi, i ricercatori hanno collaborato durante sei crociere estive congiunte. Tale collaborazione internazionale si è rivelata di grande importanza personale e professionale per tutti i ricercatori e per tutte le istituzioni coinvolte nel progetto, ma resta da evidenziare quale sia stato il contributo scientifico di tale collaborazione. A tale scopo i ricercatori hanno confrontato gli obiettivi che si erano posti all'avvio del progetto con la loro visione attuale della ricerca dello zooplancton gelatinoso. Il loro punto di vista è stato influenzato anche dal lavoro svolto all'esterno del progetto, ma nell'articolo vengono presentate le ricerche svolte nell'ambito del progetto Meduza, che hanno ampliato le loro prospettive in tre maggiori aree di ricerca: modalità di propulsione, meccanismi di predazione e significato trofico delle meduse.

Parole chiave: progetto Meduza, propulsione, distribuzione, idrodinamica, alimentazione, ruoli trofici

INTRODUCTION

Project Meduza began as a collaborative effort that focused on understanding the biology and ecology of medusae. The first research planning took place in 2001. A culminating symposium that produced the series of manuscripts in this volume occurred in May, 2009. The eight intervening years involved six joint field seasons, with a host of researchers and students working together and with ship crew, local citizens and government agencies, a variety of scientific papers that have been published already, and presentations of results at a range of different scientific conferences. These have all been valuable scientific and social products of the collaborative process. But what about our initial research goal? Has collaborative work increased our knowledge of the ecological roles played by medusae?

One way to respond to that question is to compare the state of knowledge about medusae at the outset of Project Meduza with what is known now at the time of our 2009 symposium. It is important to remember that the work in Project Meduza did not occur in isolation but in the context of progress within the larger field of zooplankton studies. We sought to expand what was known, using the unique environmental advantages found in the Mljet lakes and the oligotrophic southern Adriatic Sea. Some of the details of that process have already been published, some will follow in reports gathered for this volume, and others will be published in the months and years to come. But for our present consideration, we examine the views on medusan ecology that dominated our initial planning for Project Meduza. We view these issues as falling within three major areas: swimming propulsion, predation and other interspecific interactions within the planktonic community. This discussion is biased by the origin of the manuscript from the perspective of investigators from the USA. However, it is clear that all our other collaborators influenced the process of exploration

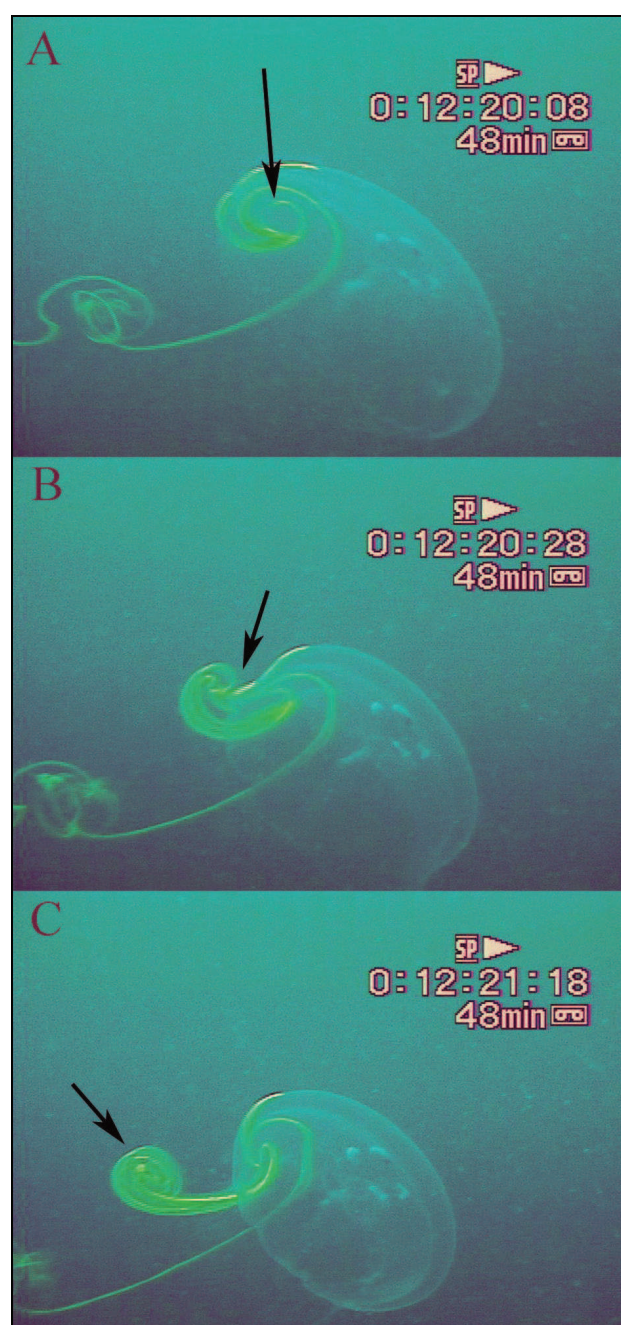
in unexpected ways and we hope these connections will be apparent.

PROPULSION AND FEEDING

Medusae are stated to be jet-propelled swimmers (Brusca & Brusca, 2003; Pechenik, 2005). A number of important correlates follow from this assumption. For example, jet propulsion is an energetically inefficient and costly propulsive mode, so jet propelled species typically have high energetic costs for swimming (Vogel,

Fig. 1: Vortice ring formation during swimming by *Aurelia aurita*, a rowing propelled scyphomedusae. (A) Relaxation phase during which the formation of the stopping vortex is visible inside the bell. (B) Start of contraction phase during which the starting vortex is forming from fluid originating both inside and outside the bell. (C) End of contraction phase with the starting vortex superstructure trailing in the wake (The vortex from the previous pulse is visible just behind it). Arrows indicate the described vortices.

Sl. 1: Prikaz vrtničnega obroča, ki nastane med plavanjem skifomeduze *Aurelia aurita*. (A) Faza sproščanja, v klobuku viden ustavljač vrtinec. (B) Začetek faze krčenja, vrtinec se oblikuje iz tekočine, ki prihaja z zunanje in notranje strani klobuka. (C) Konec faze krčenja, vrtinec se razvije v vrtnično sled. (Vrtinec, ki ga je oblikoval zadnji impulz, je viden za njim.) Puščice kažejo na opisane vrtince.



1994). For that reason, medusae usually do not swim continuously, but alternate rest periods with bursts of activity (e.g. Mills, 1981). Presumably differences in prey selection would depend primarily on the type and positioning of tentacles (Madin, 1988) as well as the types of nematocysts found on the tentacles (Purcell & Mills, 1988). These were the widely accepted concepts in 2001 when Project Meduza began. Many are still widely accepted in 2009.

Do these perceptions accurately reflect reality? There were some reports in the literature that many common medusae swam continuously and, rather than waiting in ambush for prey, used feeding currents to entrain prey to their capture surfaces (Costello & Colin, 1994, 1995). These concepts were present in the medusan literature and even included in some authoritative texts at the start of Project Meduza (e.g. Arai, 1997), but those observations still had not been incorporated into major invertebrate zoology textbooks (cited above). Part of the signifi-

cance of the issue of capture mechanics was that it broadened the consideration of prey selection by continuous swimmers, such as scyphomedusae, from capture surfaces and nematocysts to include predator-prey encounter processes. The vulnerability of prey to medusan feeding currents – and hence prey escape behavior – then became crucial for understanding prey selection by such medusae. However, this re-framing of medusae prey capture mechanisms lacked a full hydrodynamic model of the interaction between fluid motions used for propulsion compared to those used for feeding. The earliest attempts at describing oblate medusan flow patterns resulted in forcing them into conventional jet propulsion models (e.g. Costello & Colin, 1994, 1995) that were inadequate descriptions of swimming (Colin & Costello, 2002). The absence of a more detailed description of propulsive mechanics by oblate medusae hindered acceptance of the concept that medusae may have more than one mode of swimming propulsion. In fact, with-

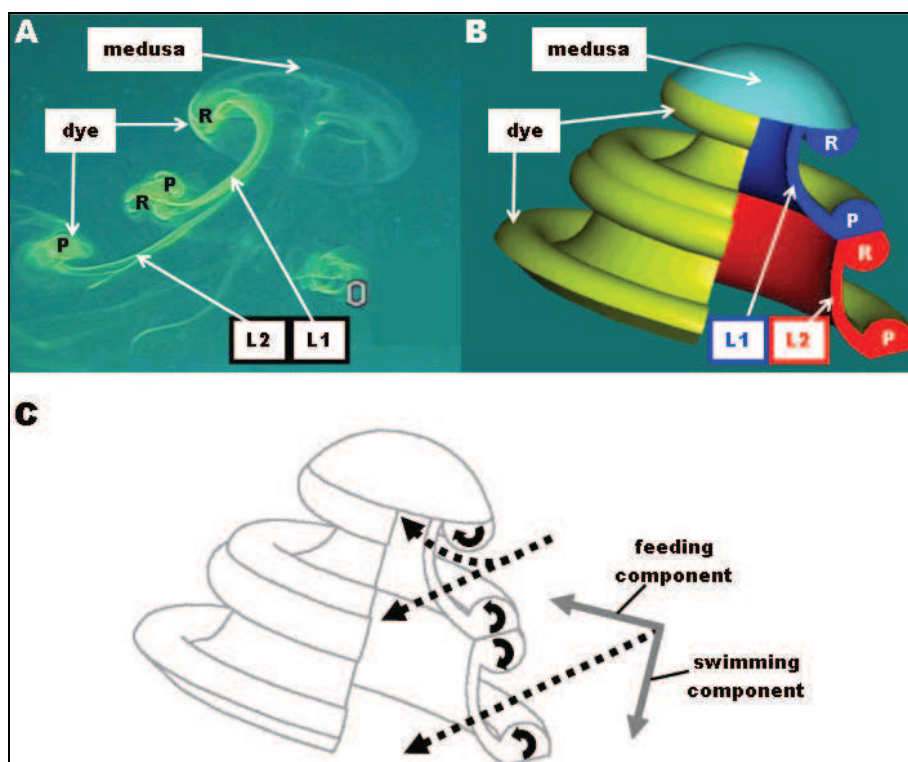


Fig. 2: (Right) Kinematics of the starting, stopping and co-joined lateral vortex structures. (A) Image of medusa vortex wake. (B) Corresponding schematic of medusa vortex wake: P – power stroke starting vortex ring; R – recovery stroke stopping vortex ring; L1/L2 – adjacent lateral vortex superstructures; (C) Flow paths in vortex wake. Solid arrows indicate directions of vortex rotation; broken arrows, flow induced by vortex rotation (from Dabiri *et al.*, 2005).

Sl. 2: (desno) Kinematika začetnega, končnega in veznega bočnega vrtilinca. (A) Slika vrtilinčne sledi meduze. (B) Shematični prikaz vrtilinčne sledi meduze: P – potisk, ki sproži vrtilinec; R – povratni gib, ki zaustavi vrtilinec; L1/L2 – struktura veznega bočnega vrtilinca. (C) Pretok v vrtilinčni sledi. Polne puščice prikazujejo smer rotacije vrtilinca; prekinjene puščice pa tok, ki ga povzroča rotacija (po Dabiri *et al.*, 2005).

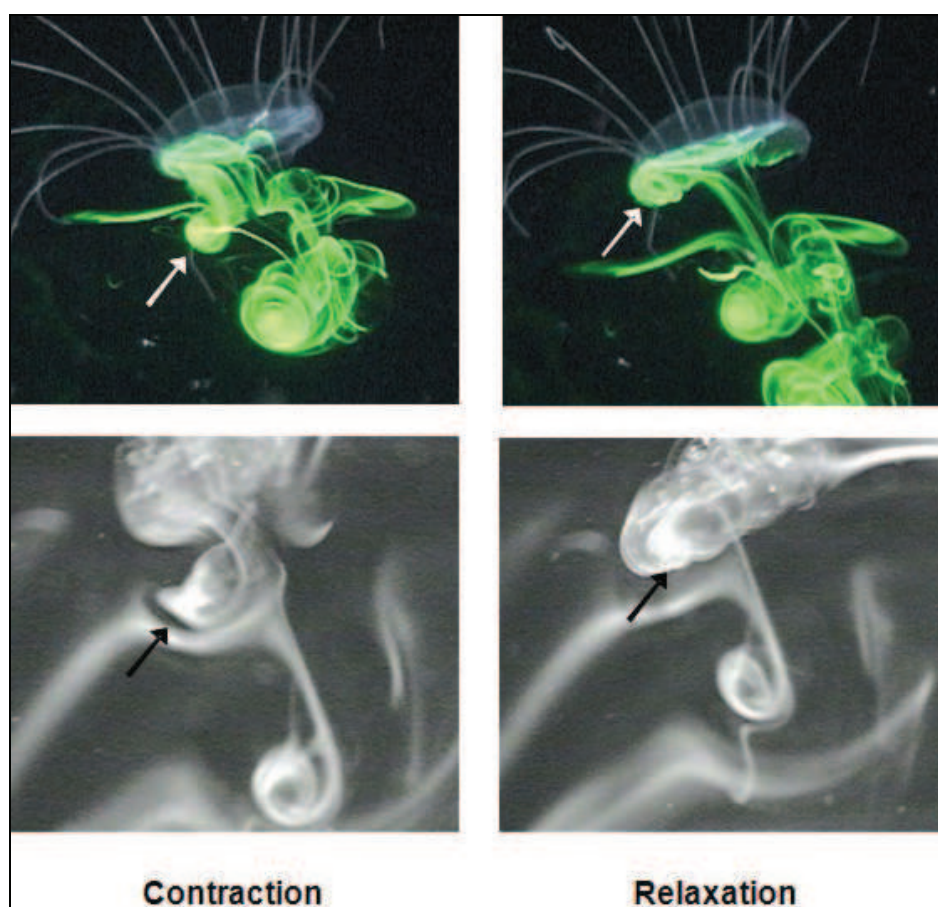


Fig. 3: *Solmissus albescens* and *Nausithoë punctata*. Flow generated by (A, B) *S. albescens* and (C, D) *N. punctata* during contraction (left-hand photos) and relaxation (right-hand photos) phases of the swimming cycle. Arrows point to the starting vortices in left-hand and to stopping vortices in right-hand photos (from Colin *et al.*, 2006).

Sl. 3: *Solmissus albescens* in *Nausithoë punctata*. Tok, ki ga povzročata (A, B) *S. albescens* in (C, D) *N. punctata* med fazo krčenja (fotografije levo) in sproščanja (fotografije desno) znotraj plavalnega cikla. Puščice kažejo na začetne vrtince na fotografijah levo in končne vrtince na fotografijah desno (po Colin *et al.*, 2006).

out an adequate mechanical model, some investigators entirely rejected alternatives to classical jet propulsion by medusae (e.g. McHenry & Jed, 2003).

The resident population of *Aurelia aurita* sp. 5 (Dawson & Jacobs, 2001) in the marine lake of Mljet Island (Big Lake, Southern Adriatic) provided the stage for a series of *in situ* flow visualization experiments that finally resolved the relationship between flow and feeding interactions for oblate rowing medusae. Aided by high water clarity and ideal SCUBA diving conditions, divers were able to precisely locate visible dyes within flows generated by medusae (Fig. 1). These methods avoided laboratory wall artifacts generated within aquariums and provided a broad mechanistic model for starting-stopping vortex interactions (Fig. 2) that we now know underlie the high propulsive efficiency and food gathering capabilities of oblate scyphomedusae (Dabiri *et al.*,

2005). Further, the hydrodynamic patterns found for *A. aurita* were demonstrated to be a useful model for species that were oblate rowers but maintained tentacles orientation towards the aboral surface (termed upstream rowers, Fig. 3).

These descriptions therefore expanded the picture of medusan propulsive and feeding interactions (Costello *et al.*, 2008) that existed before Project Meduza. This mechanical understanding served as a basis for further ecological work demonstrating unexpected links between *A. aurita*, zooplankton and the microbial communities at Mljet (Turk *et al.*, 2008) because it explained prey ingestion in terms of water processing rather than solely nematocyst activation. Both processes are necessary components of medusan predation; neither alone is sufficient to explain observed patterns.

PREDATION

Although some medusae harbor zooxanthellae as part of a mutualistic symbiosis (e.g. the genera *Cassiopea* and *Linuche*), medusae more typically prey upon other metazoans. However, oligotrophic open sea systems can present nutritional challenges for medusae because metazoan prey are often scarce. Yet, surprisingly, a number of small hydrozoan species successfully persist in these environments (Gili *et al.*, 1987; Benović *et al.*, 2005; Lučić *et al.*, 2009) (Fig 4). By examining the gut contents of the trachymedusa *Aglaure hemistoma*, we found that these small medusae consume a variety of protists in addition to metazoans (Fig. 5). The protistan prey are invisible in preserved specimens because most of them disintegrate in fixatives such as formaldehyde. *A. hemistoma* is cosmopolitan and found in oligotrophic

surface waters in several oceans and its vertical distribution patterns in the southern Adriatic Sea probably reflect its feeding ecology throughout oceanic surface waters. In those clear waters, the ability to utilize a wide range of prey appears to have been advantageous.

Subsequently, research with other small hydromedusae has shown this type of omnivory to be relatively rare because the prey handling component of the feeding process limits consumption rates (Regula *et al.*, 2009). However, *A. hemistoma* compensates for this potential disadvantage with extremely rapid prey handling capabilities (Colin *et al.*, 2005). Other coastal hydromedusae do not appear to be similarly capable. An important consequence of research with *A. hemistoma* was an increased awareness of the possibility of medusan omnivory and an expansion of the range of alternatives considered for hydromedusan feeding.

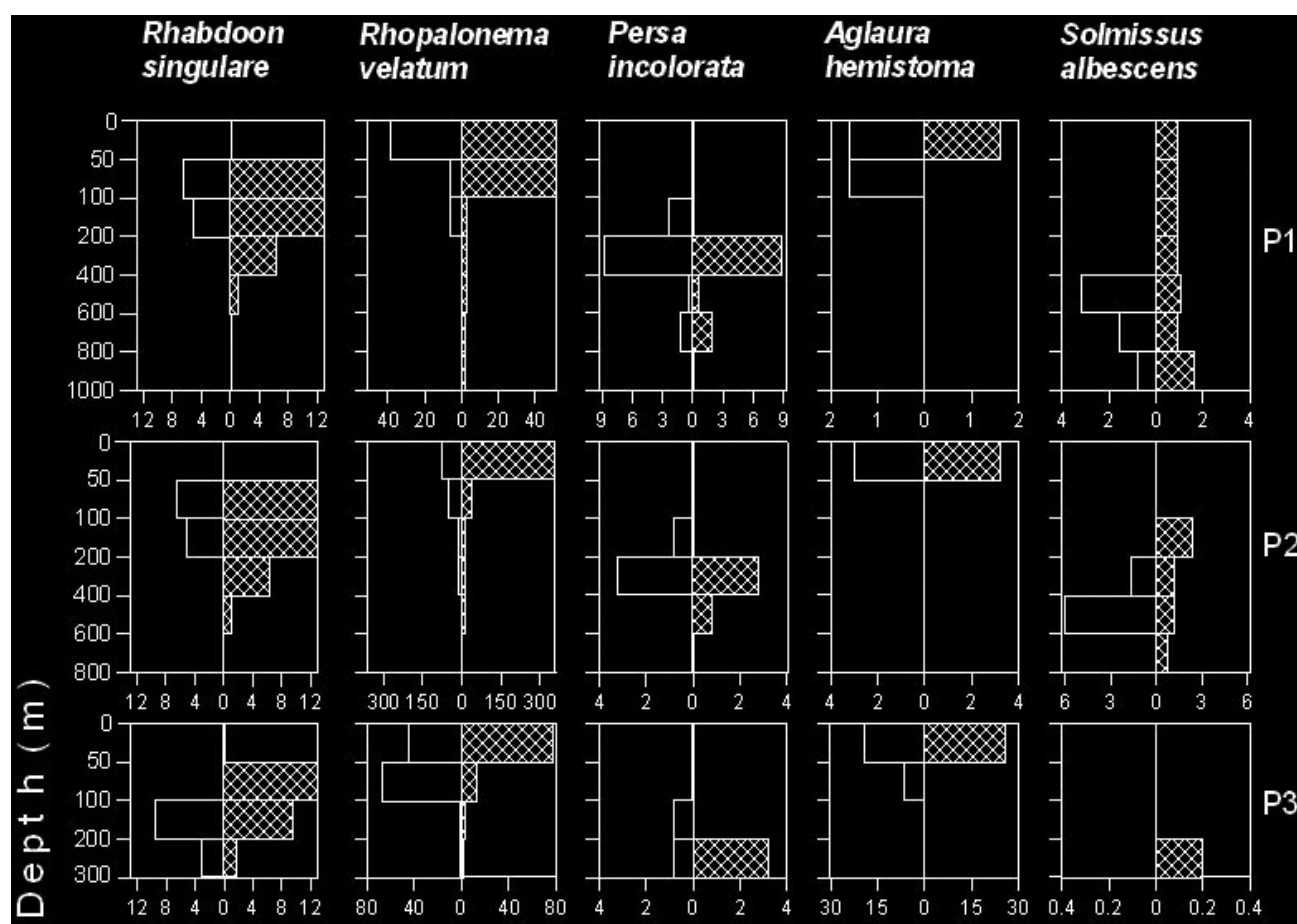


Fig. 4: Day-night vertical distribution of dominant medusae species (number of individuals 10 m^{-3}) in the middle and south Adriatic. Open bars, day samples; hatched bars, night samples (from Benović *et al.*, 2005).

Sl. 4: Dnevno-noćna vertikalna razporeditev dominantne vrste meduz (število osebkov 10 m^{-3}) v srednjem in južnem Atlantiku. Beli stolpci, dnevni vzorci; vzorčasti stolpci, nočni vzorci (po Benović *et al.*, 2005).

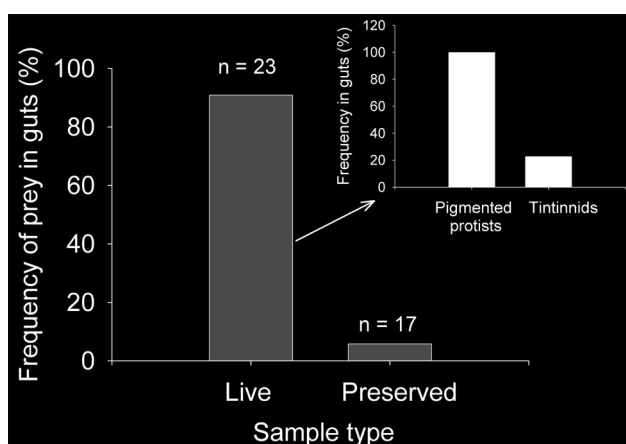


Fig. 5: Gut contents of the trachymedusa *Aglaura hemistoma*. (A) Frequency of gut contents in live and preserved (5% formaldehyde solution) *A. hemistoma* from the same date and site in the Adriatic Sea. (B) Frequency of guts of live *A. hemistoma* examined within 0.5 h of collection containing particular prey types (from Colin *et al.*, 2005).

Sl. 5: Vsebnost črevesa trahimeduze *Aglaura hemistoma*. (A) Frekvenca pojavljanja plena v črevesih živih in konzerviranih (5% raztopina formaldehida) *A. hemistoma*, ulovljenih istega dne in z istega mesta v Jadranskem morju. (B) Frekvenca pojavljanja posameznih skupin plena v črevesih živih trahimeduz *A. hemistoma*, pregledanih v roku pol ure od ulova (po Colin *et al.*, 2005).

TROPHIC ROLES

Perception of the trophic roles played by medusae has been dominated by their predatory impacts, generally on metazoan prey. But is it really that simple? Project Meduza broadened this conversation about one of the most studied medusae, *Aurelia aurita*.sp. 5. In the big lake of Mljet, *A. aurita* does not impact just the mesozooplankton it consumes, but also the microzooplankton, and ultimately, the microbial community influenced by *A. aurita*'s prey (Fig. 6). Hence, the predatory impact of *A. aurita* cascades downward through the planktonic community. But is their impact only top-down? Do they interact with higher levels of the community such as fish? One advantage of an enclosed system such as the big lake of Mljet is that members of the community are not advected throughout coastal or oceanic areas too large to sample comprehensively.

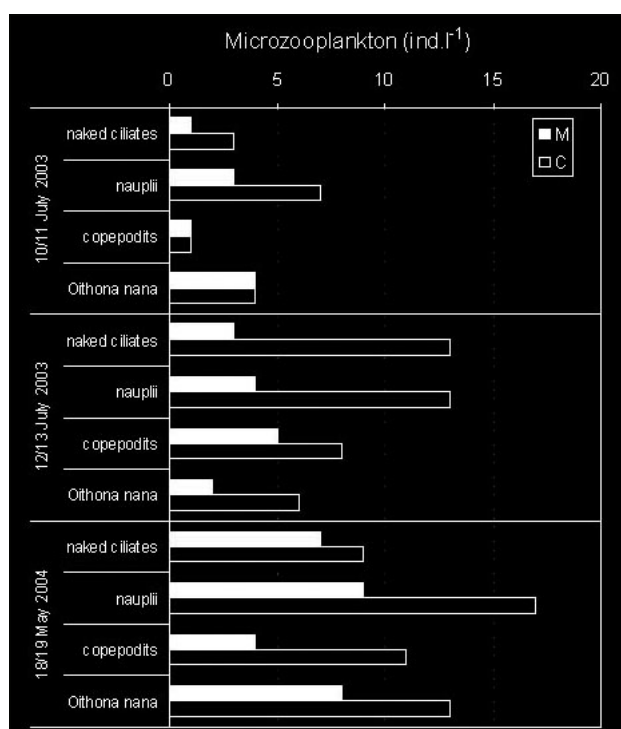


Fig. 6: Abundance of dominant microzooplankton taxa in enclosures with the presence (M – dark shaded bars) and absence (C – clear bars) of *Aurelia aurita* at the end of in situ incubation in July 2003 and May 2004 (from Turk *et al.*, 2008).

Sl. 6: Številčnost dominantnih mikrozooplanktonskih vrst s prisotnostjo (M – temni stolpci) in odsotnostjo (C – svetli stolpci) *Aurelia aurita* na koncu in situ inkubacije julija 2003 in maja 2004 (po Turk *et al.*, 2008).

The high temporal and spatial resolution of acoustic methods has allowed documentation of the rhythmic diurnal vertical migrations of both fish and scyphomedusae in an enclosed lake environment (Fig. 7). The precise nature of what drives these vertical migration patterns now needs resolution. However, the observation of these variations is the beginning of understanding the interplay between members of the lake community. Direct observation of fish-size bite marks in *A. aurita*'s exumbrellar surfaces (Graham *et al.*, 2009) suggest that fish predation may drive the downward nocturnal migration of *A. aurita* in the lake. If so, then *A. aurita*'s role as prey may become as interesting as that of predator. In this, as with the other major areas discussed here, the role of Project Meduza has served to broaden the understanding of medusae in planktonic systems.

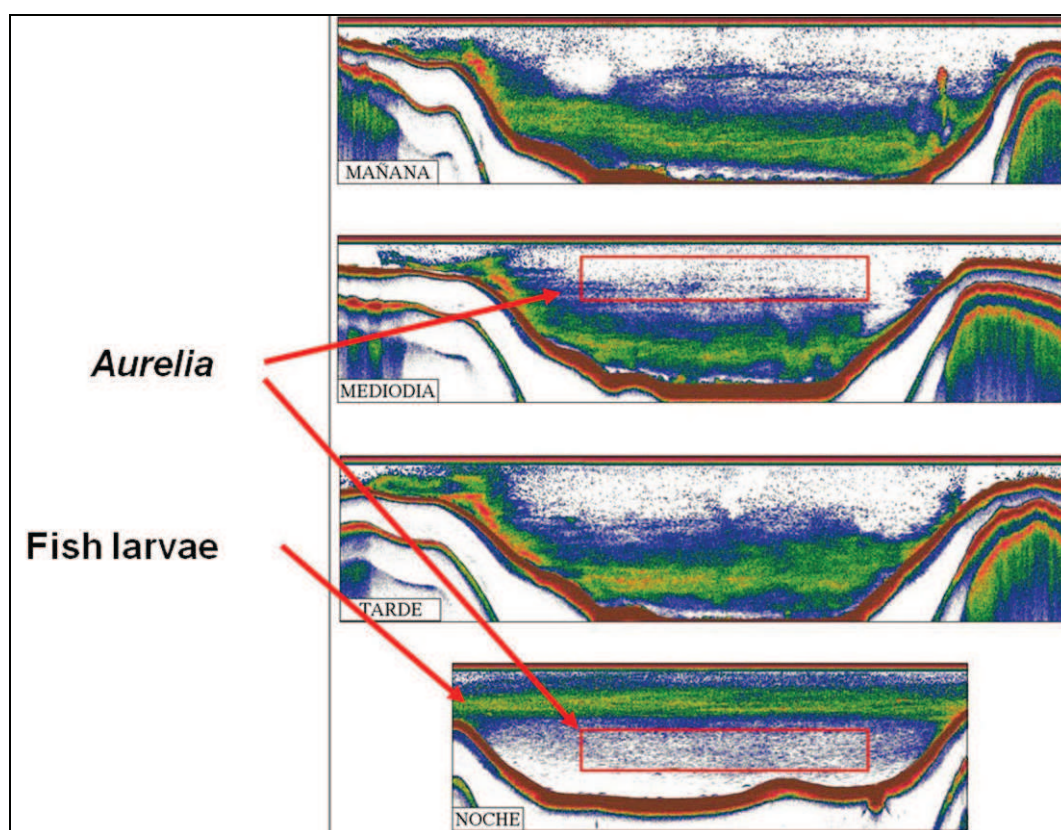


Fig. 7: Acoustic record of inverse depth relationships between fish larvae and the medusa *Aurelia aurita* in the big lake, Mljet Island, Croatia (Mianzan *et al.*, unpubl. data).

Sl. 7: Akustični posnetek obratnega globinskega sorazmerja med ribjimi ličinkami in meduzo *Aurelia aurita* v velikem jezeru, otok Mljet, Hrvatska (Mianzan *et al.*, neobjavljeno).

SUMMARY

The results described here and in the following reports from other Meduza participants demonstrate that scientific discovery is a powerful means of building international community.

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POVZETEK

Leta 2001 je Nacionalna znanstvena fundacija (National Science Foundation) iz ZDA v povezavi s hrvaškim in slovenskim ministrstvom za znanost podprla mednarodno sodelovanje, ki se je razvilo v Projekt Meduza. Vključeni raziskovalci, ki so se na pobudo z veseljem odzvali, so imeli preprost osnovni cilj – s skupnim delom razviti znanstveno raziskovanje meduz v vodah južnega Jadranskega morja. V naslednjih osmih letih je bilo izvedenih šest skupnih poletnih raziskovalnih ekskurzij. Čeprav je bilo to mednarodno sodelovanje tako na osebni kot tudi profesionalni ravni za vse raziskovalce ter vključene institucije zelo pomembno, se vendarle moramo vprašati, kaj je prineslo v znanstvenem smislu. Odgovora na to vprašanje so se avtorji lotili s primerjavo načrtanih ciljev na samem začetku dela ter tem, kako po izvedenem projektu vidijo raziskovanje želatinoznega zooplanktona. Na njihova stališča je seveda vplivalo tudi delo izven projekta, a v pričujočem članku predstavljajo raziskave v okviru projekta, ki so bistveno razširile njihove poglede na tri glavna raziskovalna področja: načini premikanja, plenjenje in prehrabeni pomen meduz.

Ključne besede: projekt Meduza, gibanje, porazdelitev, hidrodinamika, prehranjevanje, prehrabene vloge

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CLIMATE AND MEDITERRANEAN JELLYFISH: ASSESSING THE EFFECT OF TEMPERATURE REGIMES ON JELLYFISH OUTBREAK DYNAMICS

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ABSTRACT

We analyzed a 27-year time series of gelatinous carnivorous zooplankton occurrence to assess the effect of different temperature regimes on abundance. The relationship between temperature and population size of gelatinous carnivores is discontinuous and no statistical relationship was found for low temperature regimes. However, prolonged exposure to high temperatures did alter population outbreak dynamics. In particular, high temperatures and strong water column stratification were related significantly to the development of massive populations of gelatinous carnivores. These results underline the importance of gelatinous carnivorous zooplankton as ecological indicators of ecosystem change in the Mediterranean Sea.

Key words: climate change, Mediterranean Sea, temperature regime, gelatinous carnivorous zooplankton, outbreaks

CLIMA E MEDUSE MEDITERRANEE: VALUTAZIONE DEGLI EFFETTI DEI REGIMI DI TEMPERATURA SULLA DINAMICA DI ESPLOSIONE DELLE MEDUSE

SINTESI

Gli autori hanno analizzato una serie di 27 anni di segnalazioni di zooplancton gelatinoso carnivoro al fine di accertare l'effetto di differenti regimi di temperatura sull'abbondanza. La relazione fra la temperatura e la grandezza della popolazione dei carnivori gelatinosi è discontinua e non è stata riscontrata alcuna significatività statistica per regimi di bassa temperatura. In ogni caso, esposizioni prolungate ad alte temperature hanno alterato la dinamica di esplosione della popolazione. In particolare, alte temperature ed una forte stratificazione della colonna d'acqua sono state significativamente relazionate allo sviluppo massiccio delle popolazioni dei carnivori gelatinosi. Questi risultati sottolineano l'importanza dello zooplancton gelatinoso carnivoro quale indicatore ecologico di cambiamenti nell'ecosistema del mare Mediterraneo.

Parole chiave: cambiamenti climatici, mare Mediterraneo, regime di temperatura, zooplancton gelatinoso carnivoro, esplosioni

INTRODUCTION

Synergies between ecosystem degradation, overexploitation and climate change may drastically alter ecosystem dynamics as well as the resources and services they provide. Understanding how these factors interact to affect marine populations is a challenge for global ecology. In recent years, outbreaks of gelatinous carnivores have been documented in many coastal areas worldwide (Mills, 2001; Purcell, 2005). Although the occurrence of this phenomenon is a common feature of their population dynamics, the apparently enhanced recent increase in frequency and intensity of gelatinous carnivore blooms has warned scientists on the possible consequences (CI-ESM, 2001). Proliferations of gelatinous carnivore populations have a wide range of ecological implications, including alteration of entire plankton assemblages through both top-down and bottom-up effects (Pitt *et al.*, 2007; West *et al.*, 2009a, b). Their massive blooms also hamper fishing activities by clogging and bursting trawl nets (Graham *et al.*, 2003; Xiang *et al.*, 2005). They impact tourists through beach closures (Richardson *et al.*, 2009, and references therein), and their contact may cause allergic and toxic reactions in bathers (Burnett, 2009). The reported recurrent massive proliferations of gelatinous plankton during the last decade may alter the entire ecosystem dynamics (Hay, 2006).

There is also growing evidence that inter-annual and long term climate changes affect plankton communities and marine ecosystem (Hays *et al.*, 2005). The Mediterranean basin is affected by both subtropical and North Atlantic climates (Reddaway & Bigg, 1996) and it reflects secular trends of Northern Hemisphere temperature (Bethoux *et al.*, 1990). Quantifying the impact of climate regime changes on marine populations is needed to implement sound ecosystem management policies.

Here we evaluate a 27-year record of gelatinous zooplankton abundance in relation to temperature and demonstrate that high water temperature and size of gelatinous carnivore populations are related.

METHODS

Physical data. Averaged monthly data of sea surface temperature (SST) from 45° to 41° N, and from 0° to 20° E were used as a proxy of climate forcing. The dataset used was from the National Center for Environmental Prediction- National Center for Atmospheric Research (NCEP–NCAR) gridded reanalysis during the period 1950–2000 (Kalnay *et al.*, 1996). In addition, weekly water temperature records in the northern Ligurian Sea at 1, 20, 50, and 75 m depth, were used to investigate the long term variability of water column stratification.

Biological data. Data analyzed cover the years 1967 to 1993. Throughout this period, plankton was sampled

at weekly intervals from a depth of 80 m (Point B: 43°41'N; 7°19'E) in the Ligurian Sea (north-west Mediterranean). Details of sampling locality are given in Molinero *et al.* (2005). Sampling was performed by means of vertical hauls of a zooplankton net (Juday-Bogorov, 330 µm mesh size) from bottom to surface. The gelatinous carnivores analyzed were the holoplanktonic hydromedusae *Liriope tetraphylla*, *Solmundella bitentaculata*, and *Rhopalonema velatum* and the siphonophores *Abylopsis tetragona* and *Chelophyes appendiculata*. All these species are common inhabitants of the Western Mediterranean basin. The mesh size of the net prevented assessments of individuals smaller than 330 µm, but the total number of samples collected was considerable (1405 samples), and consistency of sampling and quantification protocols produced a biological data set that we believe to be comparable through time.

Data analysis. Time series were log-transformed and analysed in standardized and non-dimensional form (*i.e.* zero mean and unit variation). Statistical analysis was performed using Matlab Software.

The inter-annual variability of seasonal SST gradient between winter (JFM) and summer (JAS) was calculated and used as a proxy of environmental variability. Long term records of SST identify alterations in pelagic ecosystems, particularly with changes in phytoplankton community structure (Richardson & Schoeman, 2004). We further calculate the thermal stratification of the water column as the average temperature difference m⁻¹ of the 0–75 m depth layer.

The cumulative sum of the standardized time series (*z*-scores) was used to assess periods of similar variability. The method consists of plotting the cumulative sum of *z*-scores. Each data point, *y_t*, corresponding to time *t* (*t* from 1 to *n*) was added to the preceding data point. A constant deviation from the mean of the time series shows a constant slope on the chart, and interpretation is based on the slope of the line. Persistent changes from the mean of the time series cause a persistent change of the slope. The cumulative sum allows detecting in a simple way the timing of changes and homogeneous periods in a time series.

The effect size of temperature treatment on the gelatinous carnivore population was investigated for 1967–1993 and for each temperature regime identified. Pearson product moment correlations, as well as the probability density distribution of correlation coefficients after bootstrap resampling were computed. The analysis involved a random pairwise sampling with replacement where each time series was resampled 5,000 times. The number of elements in each bootstrap sample equals the number of elements in the original data set. The probability density distribution of the corresponding correlation coefficients was computed using nonparametric Kernel smoothing.

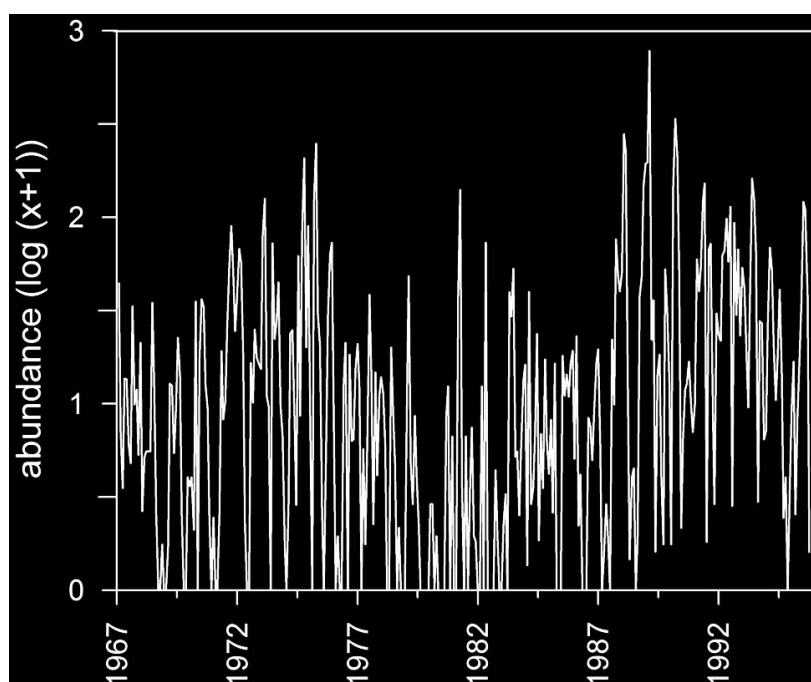


Fig. 1: Long-term variability of the abundance of holoplanktonic gelatinous carnivore species. Abundances are expressed as $\log_{10}(x+1)$.

Sl. 1: Dolgoročna variabilnost številčnosti holoplanktonskih želatinoznih mesojedih vrst. Številčnost je izražena kot $\log_{10}(x+1)$.

The dynamics of gelatinous carnivore outbreaks was assessed by means of peak-to-peak plots (Rinaldi *et al.*, 2001). The method consists in extracting from the time series, y , significant peaks (*i.e.* outbreaks), say y_i ($i = 0, 1, 2, \dots, n$), and plot them one against the previous one, thus obtaining a set of points (y_i, y_{i+1}) . The points in the peak-to-peak plot (PPP) lie on a closed regular curve (the slice of a torus) when the dynamics of the phenomenon is quasiperiodic and lie roughly on a curve when the attractor is a low-dimensional strange attractor.

RESULTS AND DISCUSSION

The inter-annual variability of the gelatinous carnivore community displays a high intermittency and two dome-shaped periods, before and after the early 1980s (Fig. 1). High abundances (peaks) indicating outbreaks were recorded throughout the investigated years. However, before the early 1980s, a higher number of events with low or null abundances were observed, whereas after the early 1980s permanently high values characterized the gelatinous carnivore abundance, and the number of events with low or null abundances was significantly reduced.

The inter-annual variability of the temperature difference between winter (JFM) and summer (JAS) in the northern Mediterranean over the second half of the twentieth century is shown in figure 2a. Values are ex-

pressed as standard deviations from the long term mean of the time series. The variability of the signal reveals two major regimes of temperature that were characterized by lower values than the long-term mean, from 1950 to the late 1970s, and higher ones after the early 1980s. A remarkably similar pattern is observed in the water column stratification during the years 1967–1993 (Fig. 2b), which also show generally low values before the early 1980s and higher values afterwards. The link between large- and local-scale temperature variability was statistically significant, as shown by the Pearson's correlation coefficient and the effective probability after correction for temporal autocorrelation ($r = 0.66$; $p < 0.05$). The cumulative sum of z-scores depicted the main temperatures regimes that characterized the pelagic environment for gelatinous carnivores. Such regimes were used afterwards as treatment effect.

The relationship between variations in the population size of gelatinous carnivores and temperature is shown in figure 3a. Considering the whole period, the Pearson's correlation coefficient and the effective probability after correction for temporal autocorrelation were $r = 0.50$ and $p < 0.05$, respectively, although the probability density estimation of correlation coefficients obtained after bootstrap resampling (5000 times) revealed a high variability in the link (mean = 0.42; std = 0.30). However, analysis of the relationship during the regime of low temperatures does not provide statistical support

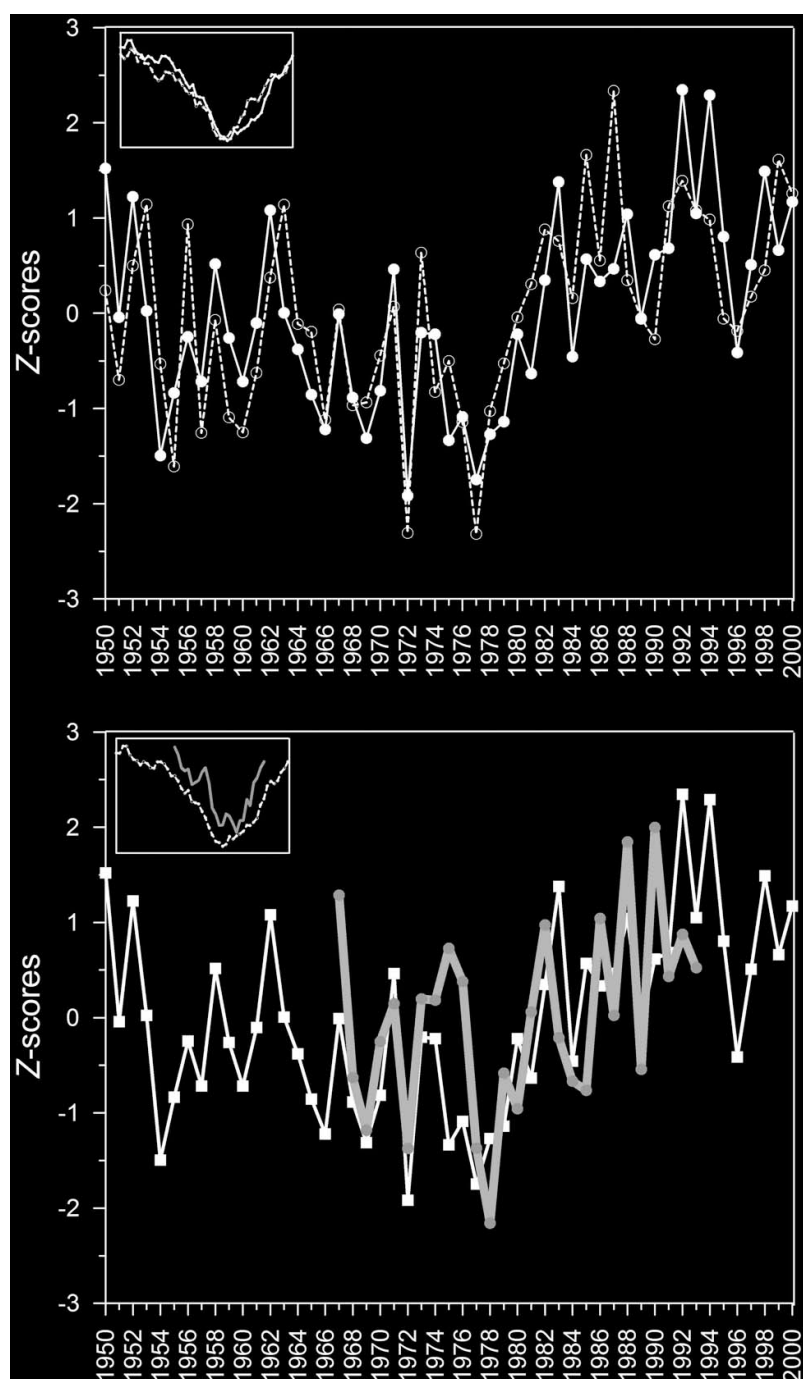


Fig. 2: (a) Inter-annual variability of the seasonal sea surface temperature (SST) gradient between winter (JFM) and summer (JAS). The time series was obtained from mean (dotted line) and maximum (continuous line) seasonal values. (b) Time series of SST gradient (mean values) and thermal stratification of the water column (0–75 m; grey line). The cumulative z-scores diagram of the time series (inset) illustrates the inflexion point that separates the two temperature regimes in the northern Mediterranean.

Sl. 2: (a) Medletna variabilnost gradienta sezonske površinske temperature morja (SST) med zimo (JFM) in poletjem (JAS). Časovni razpored je bil narejen na podlagi srednjih (črtkana črta) in najvišjih (polna črta) sezonskih vrednosti. (b) Časovni razpored SST gradienta (srednja vrednost) in termalne stratifikacije vodnega stolpa (0–75 m; siva črta). Kumulativni diagram časovnega razporeda (vloženi graf) prikazuje prevoj, ki ločuje dva temperaturna režima v severnem Sredozemlju.

Tab. 1: Relative abundance of gelatinous carnivore species in the thermal regimes investigated. The structure led by the species contribution to the total abundance is similar in the two periods, with *L. tetraphylla* and *R. velatum* as the dominant species in the two periods.

Tab. 1: Relativna številčnost želatinoznih mesojedih vrst v obravnavanih temperaturnih režimih. Struktura s prispevkom vrste k polni številčnosti je podobna v obeh obdobjih, z vrstama *L. tetraphylla* in *R. velatum* kot dominantnima vrstama v obeh obdobjih.

	Period 1 (1967–1980)	Period 2 (1981–1993)
<i>Rhopalonema velatum</i>	23.83	18.73
<i>Liriope tetraphylla</i>	61.19	57.12
<i>Solmundella bitentaculata</i>	3.81	9.55
<i>Chelophyes appendiculata</i>	6.77	11.39
<i>Abylopsis tetragona</i>	4.40	3.21

that variations in population size of gelatinous carnivores are related to temperature, as illustrated by the probability density estimation of correlations coefficients (Fig. 3a; mean = 0.26; std = 0.46). In contrast, during the high temperature regime the link was significantly enhanced and the population size changes were closely coupled to temperature variations (Fig 3a; mean = 0.57; std = 0.30). These results suggest that the relationship of gelatinous carnivores with temperature evolves according to the strength of climate signal. It is worth noting that the structure led by the species contribution to the total abundance is similar in the two periods, with *L. tetraphylla* and *R. velatum* as the dominant species in the two periods (Tab. 1).

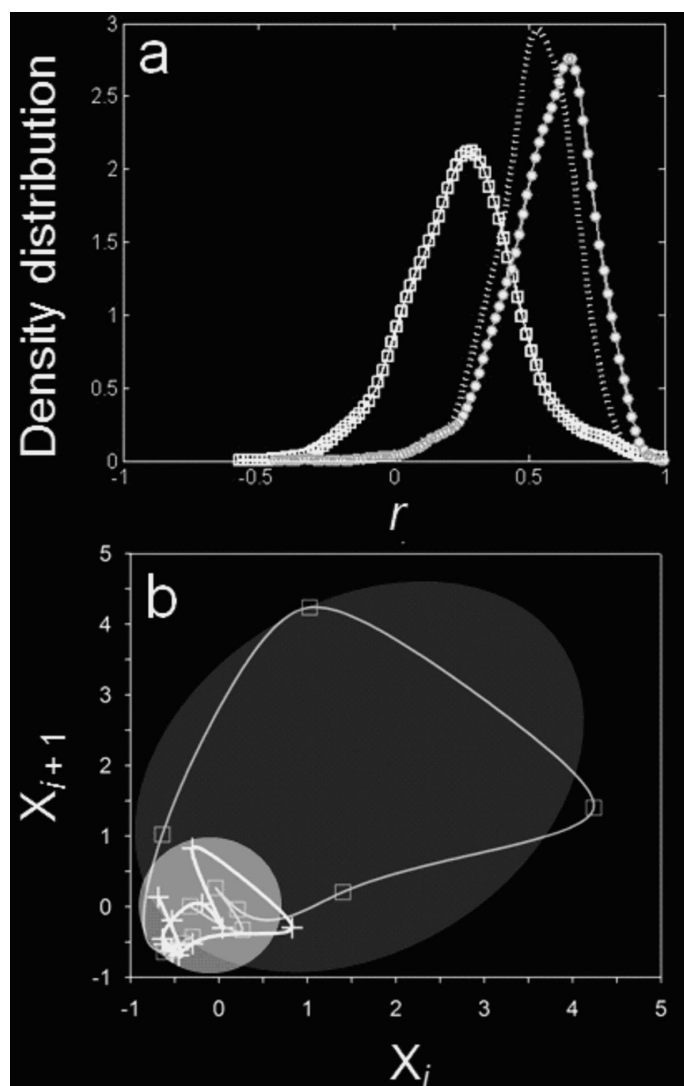


Fig. 3: (a) Probability density estimation of the correlation coefficients between temperature and the population size of gelatinous carnivores. The density distribution was obtained by bootstrap re-sampling (5,000 times) in the whole study period (dotted line) and in the two temperature regimes corresponding to the years 1967–1980 (low temperature: open symbols); and 1981–1993 (high temperature: filled symbols). (b) Long term dynamics of gelatinous carnivores outbreaks illustrated by the peak-to-peak plot, X_i , X_{i+1} , where X_i denotes a significant peak of abundance (e.g. outbreak) at time t and X_{i+1} the next significant peak at time $t+1$. The dark circle illustrates the outbreak dynamics under the low temperature regime, whereas the ellipsoid points out the new outbreak dynamics under the high temperature regime.

Sl. 3: (a) Ocena gostote verjetnosti korelacijskega koeficienta med temperaturo in velikostjo populacije želatinoznih mesojedov. Podatki za distribucijo gostote so bili pridobljeni z bootstrap vzorčenjem z vračanjem (5000-krat) tekom celotne raziskave (črtkana črta) in v dveh temperaturnih režimih v letih 1967–1980 (nizka temperatura: kvadrati); in 1981–1993 (visoka temperatura: polni krogi). (b) Dolgoročna dinamika masovnega pojavljanja želatinoznih mesojedov, prikazana z grafom vrhov X_i , X_{i+1} , kjer X_i označuje izrazit vrh številčnosti (npr. izbruh masovnega pojavljanja) ob času t in X_{i+1} naslednji izrazit vrh ob času $t+1$. Temnejši krog prikazuje dinamiko masovnega pojavljanja v nizkem temperaturnem režimu, medtem ko elipsa prikaže novo dinamiko masovnega pojavljanja v visokem temperaturnem režimu.

Although no significant changes were observed in the contribution of species to the total abundance of gelatinous carnivore population, the peak-to-peak plot unveils contrasting dynamics depending on the temperature regime (Fig. 3b). The low temperature regime showed boom cycles that were roughly described by a circle of low diameter. Conversely, the long exposure to high temperature and to the concomitant associated water column changes (*i.e.* high stratification) allowed the significant change in boom cycles. Cycles were roughly described by an ellipsoid which dimensions were 5-fold higher than the cycles noticed during the low temperature regime.

Beside the direct effect that temperature changes may have on the population dynamics of gelatinous carnivores, the observed changes are likely related to concomitant effects of climate forcing on the pelagic environment of the western Mediterranean (Menard *et al.*, 1994). For instance, Gomez & Gorsky (2005) identified modifications in the western Mediterranean related to high temperatures and high atmospheric pressure that affected changes at the bottom of the food web (*i.e.* a flagellate dominance on the microplankton community). The high temperature regime was related to persistently high values of the North Atlantic Oscillation (NAO), particularly to the longest and higher positive phase over the twentieth century. The generally warm and stable water column associated with high temperatures after the 1980s has provided suitable environmental conditions for the development of gelatinous carnivore out-

breaks (Molinero *et al.*, 2008), and substantially altered their outbreak dynamics. This is in accordance with previous investigations in the same area that found a positive relationship between the survival of gelatinous carnivore larvae and stratified water (Goy *et al.*, 1989; Buecher, 1999). These results suggest that the northern Mediterranean pelagic populations are potentially vulnerable to climate change and long term variations of gelatinous carnivore populations are indicative of ecosystem-state modifications.

In the global change context, climate projections suggest a dominance of the positive phases of the NAO (IPCC, 2007). This means that generally high atmospheric pressure, high temperatures and low wind stress are expected to dominate atmospheric conditions in the northern Mediterranean, which in turn point towards enhancement of water column stratification. As shown by our analysis, these conditions seem to alter the dynamics of gelatinous carnivore outbreaks, which may jeopardize the pelagic diversity and ecosystem function and resilience.

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PODNEBJE IN SREDOZEMSKA MEDUZE: OCENA VPLIVA TEMPERATURNIH REŽIMOV NA DINAMIKO MASOVNEGA POJAVLJANJA MEDUZ

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POVZETEK

Izvedena je bila analiza 27-letnega časovnega razporeda pojavljanja želatinoznega mesojedega zooplanktona, z namenom ocene učinka različnih temperaturnih režimov na številčnost. Razmerje med temperaturo in velikostjo populacije želatinoznih mesojedov je diskontinuirano, za nizke temperaturne režime pa ni ugotovljena statistična povezava. Je pa dinamiko masovnega pojavljanja populacije spremenilo podaljšano izpostavljanje visokim temperaturam. Še posebej visoke temperature in močna stratifikacija vodnega stolpa so izrazito povezane z razvojem masovnih populacij želatinoznih mesojedov. Ti rezultati kažejo na velik pomen želatinoznega mesojedega zooplanktona kot ekološkega indikatorja ekosistemskih sprememb v Sredozemskem morju.

Ključne besede: klimatske spremembe, Sredozemsko morje, temperaturni režim, želatinozni mesojedi zooplankton, masovno pojavljanje

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IN SITU MANIPULATION OF VERTICALLY MIGRATING GELATINOUS ZOOPLANKTON USING NIGHTTIME BLUE-WATER SCUBA IN THE SOUTH-CENTRAL ADRIATIC SEA

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ABSTRACT

Technological advances in undersea exploration (e.g., tethered cameras, remotely operated vehicles [ROVs], Autonomous Underwater Vehicles [AUVs] and manned submersibles) have opened new windows into diversity and distribution of fragile gelatinous organisms in the vast mesopelagic realm (~300 m – 1,000 m deep). While extraordinary in expanding our view of its richness, mesopelagic exploration remains largely a ‘look but don’t touch’ environment and this limits our ability to understand these animals through physical manipulation relevant to the finer scales of the individual organism. We have been conducting a series of in situ observations and manipulations using blue-water SCUBA during the night at a 1,200 m station centrally located in the southern Adriatic Sea. We report here on a suite of vertically migrating gelatinous animals, including the narcomedusa Solmissus albescens and the physonect siphonophores Forskalia formosa and Agalma elegans, whose ranges extend to the mesopelagic realm during the day, but reach SCUBA diving depths during the night. Our in situ approach combined with proximity to shore exploits the natural vertical migratory behavior of some mesopelagic species, and we therefore add to the widening spectrum of methods needed to evaluate these ecologically important yet difficult to study organisms.

Key words: vertical migration, *in situ*, behavior, hydrodynamics, Adriatic Sea, night-time SCUBA

UTILIZZO DI IMMERSIONI NOTTURNE IN ACQUE APERTE IN ADRIATICO MERIDIONALE PER ESPERIMENTI *IN SITU* CON ZOOPLANKTON GELATINOSO MIGRANTE VERTICALMENTE

SINTESI

Progressi tecnologici nelle esplorazioni subacquee (quali videocamere collegate ai PC, veicoli guidati a distanza [ROVs], veicoli subaquei autonomi [AUVs] e sommergibili con equipaggio) hanno aperto nuove finestre nella diversità e nella distribuzione dei fragili organismi gelatinosi nel vasto regno mesopelagico (~300 m – 1.000 m di profondità). La ricerca ha portato a straordinarie scoperte inerenti la ricchezza del regno mesopelagico, ma l'esplorazione è rimasta ai livelli di "guardare ma non toccare", il che limita la nostra capacità di comprendere questi animali attraverso la manipolazione fisica, adattata alla sensibilità di ogni singolo organismo. Gli autori hanno condotto una serie di osservazioni e manipolazioni in situ, durante immersioni notturne in acque aperte, in una stazione dell'Adriatico meridionale che altrimenti raggiunge i 1200 m di profondità. L'articolo riporta le osservazioni su animali gelatinosi migranti verticalmente, quali la narcomedusa Solmissus albescens ed i sifonofori Forskalia formosa e Agalma elegans, che si trattengono nel regno mesopelagico durante il giorno, ma che risalgono a profondità accessibili in immersione durante la notte. L'approccio in situ, unito alla vicinanza della costa, hanno permesso di evidenziare la migrazione verticale naturale di alcune specie mesopelagiche. Tale metodo va quindi ad aggiungersi all'ampio spettro di metodi utilizzati per la valutazione di tali organismi ecologicamente importanti e difficili da studiare.

Parole chiave: migrazione verticale, *in situ*, comportamento, idrodinamismo, mare Adriatico, immersioni notturne
SCUBA

INTRODUCTION

Gelatinous zooplankton is an important member of many marine planktonic communities, including mid- and deep-water oceanic regions. The widespread presence of this phylogenetically diverse assemblage has been documented by blue-water SCUBA techniques as well as by both manned and remotely operated vehicles (reviewed in Robison, 2004). A substantial portion of pelagic biomass maybe incorporated into the bodies of these organisms and their interactions are complex enough that they have been labeled the "jelly web" (Robison, 2004).

Although the gelatinous component of the plankton is ecologically important, much of the research on oceanic gelatinous zooplankton has been descriptive in nature due to the historically poor documentation of this group's presence in oceanic systems. Consequently, much of this work has focused on discoveries of new species, establishment of systematic and phylogenetic relationships, patterns of distribution and abundance and behavioral observations (Madin, 1988; Mills & Goy, 1988; Sørnes *et al.*, 2008). Although key aspects of their physiological ecology have been described, such as the tendency for a variety of gelatinous zooplankton to largely maintain metabolic rate with depth (Thuesen & Childress, 1994; Childress, 1995), detailed experimental manipulations with gelatinous species from below the epipelagic zone have been limited due to physical vulnerability (Dennis, 2003; Haddock, 2004; Osborn & Barber, 2004) and often unexpected physiological responses to shipboard handling (Bailey *et al.*, 1994). Consequently, deeper water species neither transport well nor survive adequately during controlled experimentation. Much more is known about more accessible epipelagic species that are also physically vulnerable but within the depth range of SCUBA (Dabiri *et al.*, 2005; Rakow & Graham, 2006). This presents a dilemma for research on mesopelagic and bathypelagic species – these are obviously ecologically important species but we are unable to study them as we do other oceanic animals due to their inaccessibility. Here we provide a summary of three years' work in what we consider a rare circumstance where predictable nocturnal migrations of largely mesopelagic gelatinous organisms occur at SCUBA depths (upper 25 m) in the south-central Adriatic Sea.

METHODS

The sampling location where we routinely encountered mesopelagic organisms at the surface at night was at the 1200 m deep station in oligotrophic waters of the south-central Adriatic Sea (42°11' N, 17°42' E) (Fig. 1), regularly visited by the 30 m Croatian oceanographic research vessel 'Naše more'. Only eight scuba dives were made during May–June in 2002, 2003 and 2005, spe-

cifically for the collection of video footage of mesopelagic animals; ship –time at night was devoted primarily to more traditional sampling techniques. All dives were timed to start just prior to maximum ascent of the vertical migrators (22:30–00:30 local time). Moon light is generally an important variable when investigating nocturnal species, but lunar phase could not be considered when scheduling cruises; details of lunar phase during our dives are provided in Table 1.

Tab. 1: Summary of nighttime blue-water dives showing the starting time of each dive and the lunar phase on that date. Dive number is the same for figure 2.

Tab. 1: Seznam nočnih potopov v velikih globinah, z začetnim časom vsakega potopa in lunino fazo na tisti dan. Številke potopov ustrezajo tistim na sliki 2.

Dive No.	Date	Time (Local)	Lunar phase
1	2 Jun 2002	22:30	1/4 (waning)
2	4 Jun 2002	22:30	1/5 (waning)
3	23 Jul 2003	23:30	1/5 (waning)
4	24 Jul 2003	00:10	1/6 (waning)
5	27 Jul 2003	00:20	1/10 (waning)
6	28 Jul 2003	00:10	New Moon
7	25 May 2005	23:20	7/8 (waning)
8	26 May 2005	23:00	7/8 (waning)

Night-time blue-water SCUBA and video collection

A variety of designs and gear exist for the use of specialized blue-water SCUBA (Hamner *et al.*, 1975; Heine, 1986; Haddock & Heine, 2005). These designs were all created with the intention of daylight operations when diver visibility was of primary concern. However, when blue-water SCUBA is used at night, there is a unique set of challenges for the divers (Haddock & Heine, 2005). Specifically, our dives were intended to maximize duration and clear video coverage, and so we used high intensity video lights on each dive. This necessarily entailed loss of darkened conditions favored by many species. In order to minimize the effect of our bright lights, individual divers (or diver pairs during manipulation studies) remained separated at the fully extended tether distance of 10 m. Additionally, working divers attempted to stay on opposite sides of the main down-line to avoid tether cross-over and re-sampling of organisms. Because working at full-tether distance from the safety diver poses additional risks of inadvertent sinking below maximum intended operating depth, we set the central trapeze at no deeper than 15 m on the main down-line. Due to remoteness of the fieldwork and narrow temporal window of vertical migrations, only one dive was conducted each night.

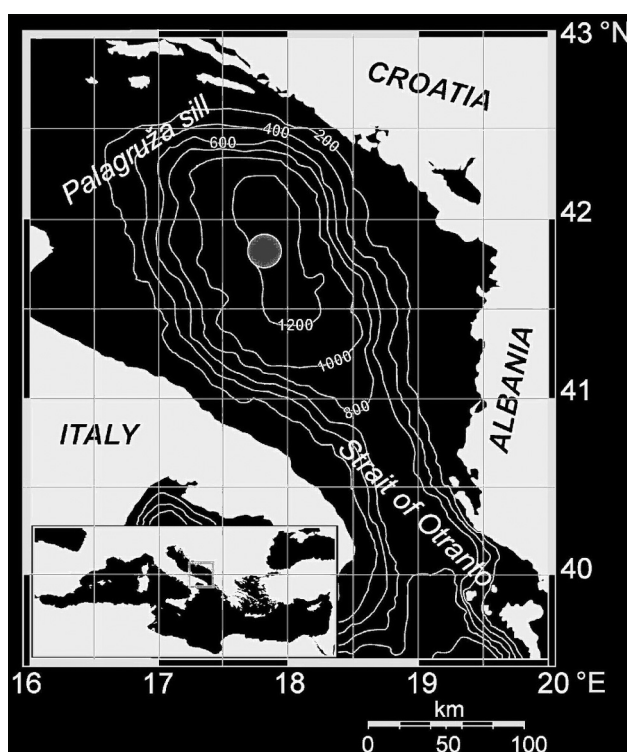


Fig. 1: Map of the study site showing the 1,200 m station in the south-central Adriatic Sea.

Sl. 1: Karta obravnavanega območja z označeno postajo na 1200 m globine v južnem delu srednjega Jadranskega morja.

During the eight dives, individual working divers used a digital video camera (Sony DCX-950, NTSC miniDV format) in a waterproof housing (Light and Motion, Inc.). Two high-intensity lights (Sun Ray HID, Light and Motion, Inc.) were turned on only while filming. Video lights were turned off to re-acclimate light sensitive animals around the divers if it was felt that lights were either attracting or distracting too many animals. We specifically targeted soft-bodied and gelatinous animals, though crustaceans and fish were common on each dive (Tab. 2). The durations of individual video sequences were limited by the length of time a tethered diver could remain with the target, and video sequences typically ranged from only a few seconds to about one minute.

All footage was reviewed in the laboratory. Individual sequences showing clearly identifiable morphologies and behaviors were isolated and archived in a video library at the Dauphin Island Sea Lab. When necessary, identification was aided by consulting taxonomic experts (as in the case of the physonect siphonophores).

Tab. 2: List of gelatinous zooplankton taxa observed and overall contribution by frequency of individual observation. Taxon number is for reference with figure 2. Identifications were made to species level unless otherwise indicated as 'unknown'.

Tab. 2: Seznam obravnavanih vrst želatinoznega planktona in splošni prispevek s frekvenco posameznih opažanj. Zaporedne številke vrste ustrezajo tistim na sliki 2. Identifikacije so bile narejene na ravni vrste, sicer je uporabljena oznaka 'neznano'.

Taxon #	Name	Contribution (%)
1	<i>Solmissus albescens</i>	39.9
2	<i>Geryonia proboscidalis</i>	3.5
3	<i>Pelagia noctiluca</i>	k1.6
4	<i>Aurelia</i> sp.	0.4
5	<i>Amphinema</i> sp.	0.6
6	Hydromedusa (unknown, small)	1.4
7	<i>Nanomia bijuga</i>	4.5
8	<i>Agalma elegans</i>	3.8
9	<i>Forskalia formosa</i>	6.6
10	<i>Athorybia rosacea</i>	0.4
11	<i>Hippopodius hippopus</i>	1.0
12	Dyphiid siphonophore (unknown)	7.6
13	<i>Salpa maxima</i> (solitary)	5.8
14	<i>Salpa maxima</i> (chain)	8.2
15	Salp (unknown)	0.7
16	<i>Pyrosoma atlanticum</i>	1.4
17	Doliolid (unknown)	3.1
18	<i>Sagitta lyra</i>	4.5
19	<i>Phylloroe</i> sp.	2.5
20	Gymnosome pteropod	0.7
21	Pseudothecosoma pteropod	0.6
22	Pteropod (unknown thecate)	0.7
23	Tomopterid polychaet (unknown)	0.7

RESULTS AND DISCUSSION

Although we only made eight night dives at this location, we nonetheless documented 23 recognizable taxonomic taxa from video (Tab. 2). Eleven of these were identifiable to species and at least one identifiable to genus. Diversity within the planktonic community was dominated by cnidarians (medusae and siphonophores = 71.2% of all observations) and pelagic tunicates (salps, doliolids and pyrosomes = 19.1% of all observations) (Tab. 2). Among the cnidarians, frequency of observation was dominated by the vertically migratory hydromedusa *Solmissus albescens* (40% of all observations). In fact *S. albescens* was highly predictable at this location as it occurred on 7 of the 8 dives (Fig. 2). Mills *et al.* (1996) accumulated a species list consisting of 35 taxa during 26 ROV dives in the northwestern Mediter-

Tab. 3: Most frequently observed gelatinous zooplankton species and their reported depth distributions. Species that have a reported mesopelagic distribution are indicated with an (*). Note that approximately 2/3 of the species commonly found in surface waters at night have previously been characterized as possessing mesopelagic distributions.

Tab. 3: Najpogostejše opažene vrste želatinoznega planktona in njihova globinska distribucija. Vrste z zabeleženo mezopelaško distribucijo so označene z (*). Približno 2/3 vrst, ki jih ponoči ponavadi najdemo v površinskih vodah, je bilo predhodno uvrščenih pod vrste z mezopelaško distribucijo.

Taxa list	Reported vertical distribution	Location	Reference
<i>Solmissus albescens</i> *	560–25 m	NW Med	Laval <i>et al.</i> , 1989; Andersen <i>et al.</i> , 1992
	1,000-surface	S Adriatic	Batistić <i>et al.</i> , 2004; Benović <i>et al.</i> , 2005
<i>Salpa maxima</i> *	surface	SW Atlantic	Sigl, 1912; Amaral <i>et al.</i> , 1997
	>300m-surface	W Med	Franqueville, 1971 (and refs therein)
<i>Forskalia formosa</i> *	~600 m	W Med	Mills <i>et al.</i> , 1996
<i>Sagitta lyra</i> *	>600 m-surface	S Adriatic	Batistić <i>et al.</i> , 2004
<i>Nanomia bijuga</i> *	surface	W Med	Mills <i>et al.</i> , 1996
	10–800 m	E Pacific	Robison <i>et al.</i> , 1998
<i>Geryonia proboscidalis</i>	surface	S Adriatic	Benović <i>et al.</i> , 2005
<i>Agalma elegans</i> *	600–300 m	W Med	Mills <i>et al.</i> , 1996; Franqueville, 1970, 1971
<i>Pyrosoma atlanticum</i> *	700–75 m	NW Med	Andersen <i>et al.</i> , 1992
<i>Hippopodius hippopus</i> *	>100 m-surface	S Adriatic, Med	Mills <i>et al.</i> , 1996; Batistić <i>et al.</i> , 2004
	400 m	W Med	Franqueville, 1970, 1971
<i>Pelagia noctiluca</i> *	surface	W Med	Mills <i>et al.</i> , 1996
	1,400 m-surface	W Med	Franqueville, 1970, 1971

anean Sea. However, the difference between our observation list and theirs is likely due to greater observation durations using ROV technology.

Ten species of gelatinous zooplankton accounted for more than 80% of all observations (Tab. 3). Nine of these species are documented as having a mesopelagic distribution. Therefore we consider their presence in the upper 25 m during our dives as a consequence of a nocturnal vertical migration as no large gelatinous plankton was observed during any preliminary daytime SCUBA dives during the first year of the study at the very same location.

Previous studies demonstrated that a diverse community of both crustacean and gelatinous zooplankton commonly occur at this particular location (Benović *et al.*, 2005; Lučić *et al.*, 2005). Yet, their presence at the very near surface remains an enigma due to low production rates and plankton standing stocks in the south-central Adriatic. Our taxonomic information along with that of Benović *et al.* (2005) and Lučić *et al.* (2005) suggests seasonal shifts in the migrating community from the spring siphonophore-rich community to the summer salp-rich community. The narcomedusa *S. albescens* was consistently common through both seasons. *S. albescens* appears to be an important predator on both siphonophores and salps as we routinely observed *S. albescens* returning to depth with guts filled with both prey types. Similar interactions between mesopelagic

dwellers have been characterized as a 'jelly web' where predator-prey interactions within the gelatinous zooplankton community partitions material flow away from

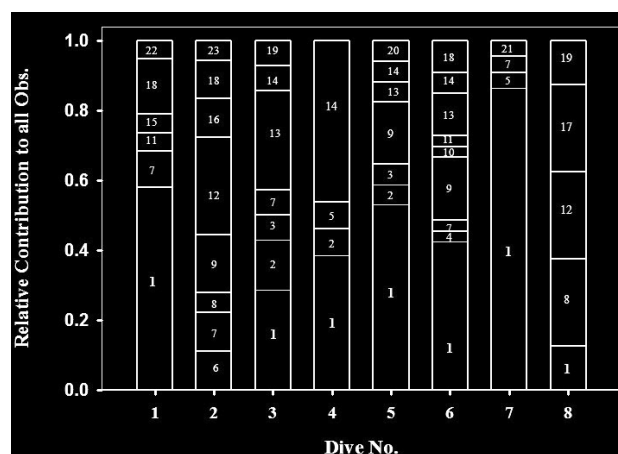


Fig. 2: Frequency of taxa observations during eight night-time blue-water dives. Dive number is the same as in Table 1. Numbers within each stacked plot indicate taxa as referenced in Table 2.

Sl. 2: Frekvenca opazovanj tekom osmih nočnih potopov v velikih globinah. Številka potopa je ista kot v Tabeli 1. Številke znotraj vsakega dela stolpca ustrezajo vrsti, navedeni v Tabeli 2.

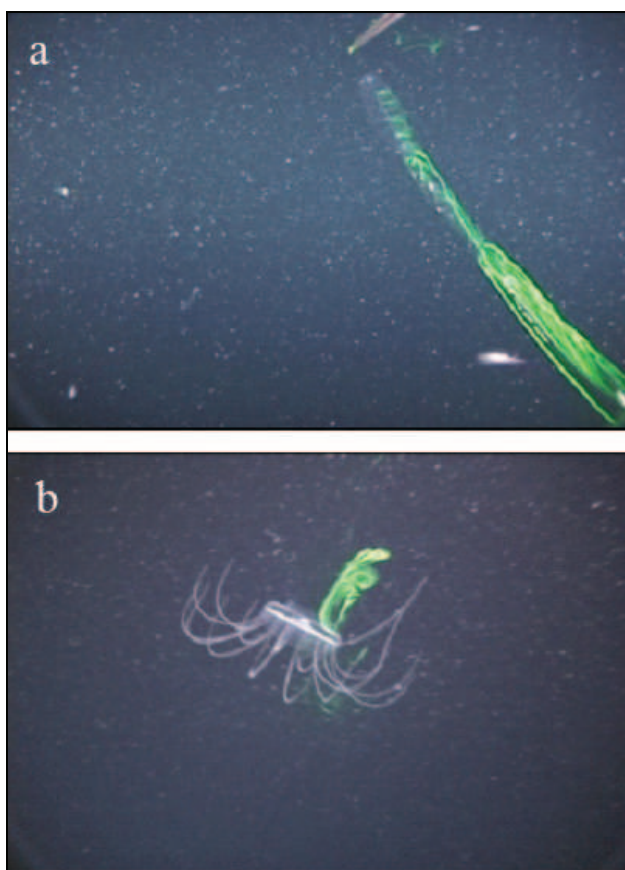


Fig. 3: Two examples of nighttime bluewater SCUBA manipulations of mesopelagic gelatinous zooplankton, (a) *Agalma elegans* and (b) *Solmissus albescens*. Wakes and vortices are visible via manual dye injection at the upstream swimming path (the diver's pipet tip is visible in the top panel).

Sl. 3: Dva primera obravnave mezopelagičnega želatinoznega planktona, (a) *Agalma elegans* in (b) *Solmissus albescens*, tekom nočnih potopov v velikih globinah. Turbulence in vrtinci so vidni zaradi brizga barve v zgornji del plavalne poti (vrh potapljačeve pipete je viden na zgornji sliki).

non-gelatinous organisms (Robison, 2004). In the present work, we documented these same mesopelagic predator-prey interactions in the south-central Adriatic Sea at depths approachable by SCUBA divers. The site is particularly valuable because the high-amplitude of the vertically migrating community is rare, if not unique, in its proximity to the shore.

A natural laboratory for manipulative investigations

Nocturnal vertical migration of otherwise mesopelagic species provided us with an opportunity to engage in direct manipulation of mesopelagic animals via SCUBA. Owing to the tactile and perceptual abilities of trained blue-water SCUBA divers, these types of manipulations are difficult or impossible with other 'remote' technologies such as cameras, ROVs, AUVs and submersibles. Previous studies of the swimming behavior of epipelagic medusae have demonstrated that divers can control and make detailed examination of swimming wakes to better understand unusual propulsive mechanisms (e.g. Dabiri *et al.*, 2005). Similarly, SCUBA access to mesopelagic species has allowed us to manipulate conditions that permit visualization and analysis of the wakes of mesopelagic species such as *Solmissus albescens* (Colin *et al.*, 2006; Fig. 3a). Furthermore, current efforts are underway with a variety of siphonophores, medusae and salps (the authors, *unpubl. data*; see Fig. 3) using these *in situ* methods and other manipulations adapted from laboratory hydrodynamic studies (e.g. Katija & Dabiri, 2008). The combination of new quantitative *in situ* approaches and access to mesopelagic species provides us the opportunity to examine the functional ecology of these gelatinous species at levels of quantification and direct manipulation that have not been previously possible. Consequently, this approach provides another tool among a growing list (Haddock, 2004; Robison, 2004) that enables researchers to evaluate these demonstrably important gelatinous animals which have been largely inaccessible for quantitative research.

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UPORABA NOČNIH POTOPOV V ODPRTIH VODAH JUŽNEGA JADRANA ZA *IN SITU* POSKUSE Z VERTIKALNO MIGRIRAJOČIM ŽELATINOZNIM PLANKTONOM

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POVZETEK

Tehnološki napredek v podvodnem raziskovanju (npr. fotoaparati in kamere z računalniško povezavo, vozila na daljinsko upravljanje (ROV), avtonomna podvodna vozila (AUV) in mini podmornice s posadko) je omogočil nov vpogled v diverziteto in razširjenost občutljivih želatinoznih organizmov v obsežnem mezopelagičnem pasu (~300-1000 m globoko). Raziskovanje mezopelagičnega območja nam je sicer izjemno razširilo pogled na bogastvo tega okolja, vendar v glavnem ostaja v okvirih opazovanja brez fizičnega dotika, kar omejuje našo zmožnost razumevanja teh živali s pomočjo fizične obravnave, ki bi ustrezala občutljivosti posameznega organizma. Opravljena je bila vrsta nočnih in situ opazovanj in obravnav s SCUBA potopi v globinah, in sicer na postaji z globino 1200 m v južnem Jadranskem morju. Obravnavana je bila skupina vertikalno migrirajočih želatinoznih živali, vključno z narkomeduzo Solmissus albescens in cevkači iz reda Physonectae Forskalia formosa ter Agalma elegans, katerih razpon sega od mezopelagičnega območja čez dan do globin, dosegljivih s SCUBA potapljanjem ponoči. Z in situ pristopom, kombiniranim z bližino obale, smo lahko sledili naravnemu vertikalnemu migriranju nekaterih mezopelagičnih vrst ter s tem prispevali v vedno širši spekter metod za evalvacijo teh ekološko pomembnih organizmov, ki pa jih je tako težko proučevati.

Ključne besede: vertikalna migracija, *in situ*, vedenje, hidrodinamika, Jadransko morje, nočno potapljanje SCUBA

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PLANKTONIC CNIDARIANS IN THE OPEN SOUTHERN ADRIATIC SEA: A COMPARISON OF HISTORICAL AND RECENT DATA

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ABSTRACT

This review compares historical data sets (1967–68, 1974–1976, 1993–1995) to the most recent data (2002–2004) on the composition, abundance, bathymetric distribution, and vertical migration of cnidarians of the deep southern Adriatic. 18 species of medusae are typical open-ocean holoplanktonic species and 6 of these were either always or frequently found in samples, namely Rhabdoon singulare, Aglaura hemistoma, Persa incolorata, Rhopalonema velatum, Sminthea eurygaster, and Solmissus albescens. The most common calycophore siphonophores are Lensia subtilis, L. meteori, Eudoxoides spiralis, Sphaeronectes gracilis, and S. irregularis followed by Hippopodius hippopus, Vogtia penthacantha, Lensia conoidea, L. fowleri, Chelophyes appendiculata, Kephyes ovata, and Bassia bassensis. Some differences in presence and abundance between historical and recent data are noted.

Key words: South Adriatic, medusae, calycophoran siphonophores, composition, abundance, bathymetric distribution

CNIDARI PLANCTONICI IN ACQUE APERTE DELL'ADRIATICO MERIDIONALE: CONFRONTO FRA DATI STORICI E RECENTI

SINTESI

L'articolo confronta serie di dati storici (1967–68, 1974–1976, 1993–1995) con quelli più recenti (2002–2004) inerenti la composizione, l'abbondanza, la distribuzione batimetrica e la migrazione verticale dei cnidari delle acque profonde dell'Adriatico meridionale. 18 specie di meduse sono tipiche specie oloplanctoniche di acque aperte; 6 di queste sono state ritrovate sempre o molto frequentemente nei campioni. Si tratta di Rhabdoon singulare, Aglaura hemistoma, Persa incolorata, Rhopalonema velatum, Sminthea eurygaster, e Solmissus albescens. I più comuni sifonofori calicofori sono Lensia subtilis, L. meteori, Eudoxoides spiralis, Sphaeronectes gracilis e S. irregularis, seguiti da Hippopodius hippopus, Vogtia penthacantha, Lensia conoidea, L. fowleri, Chelophyes appendiculata, Kephyes ovata e Bassia bassensis. Nell'articolo vengono presentate alcune differenze nella presenza e nell'abbondanza fra dati storici e recenti.

Parole chiave: Adriatico meridionale, meduse, sifonofori calicofori, composizione, abbondanza, distribuzione batimetrica

INTRODUCTION

Planktonic cnidarians are an important and often conspicuous component of the top trophic level of many marine ecosystems. Knowledge of their spatial and temporal variability and their production dynamics is essential to understand the flow of energy and cycle of materials in these systems (Persad *et al.*, 2003). Owing to the comparative difficulties of open-ocean sampling, it is not surprising that relatively fewer observations of diversity and abundance have been reported for pelagic cnidarians and other pelagic gelatinous taxa than for those in more accessible nearshore waters (Youngbluth *et al.*, 2008).

The combination of over-fishing, eutrophication, climate change, translocation, and habitat modification that have been documented over the recent years in a wide range of marine areas appear to have favoured the development of jellyfish populations over that of other marine organisms (Molinero *et al.*, 2008; Richardson *et al.*, 2009). This upsurge of jellyfish was sufficiently dramatic and wide-spread that it attracted notable scientific and even popular attention (Purcell, 2005).

This same pattern has also been reported in the Adriatic Sea, but so far only for coastal waters. For example, previously unrecorded blooms of *Muggiea atlantica* was found in the northern Adriatic (Kršinić & Njire, 2001), the formerly dominant *M. kochi* was replaced by a congener, *M. atlantica*, in the eastern southern Adriatic, and scyphomedusae, especially *Pelagia noctiluca*, underwent unusually persistent blooms along the eastern Adriatic coast (Benović & Lučić, 2001; Miloš, 2009).

Research on planktonic cnidarians has a long tradition in the Adriatic Sea (see Benović & Lučić, 1996; Gamulin & Kršinić, 2000). The open southern Adriatic Sea is one of the few parts of the Mediterranean that has been subjected to relatively constant study of cnidarians over the past 70 years (Gamulin, 1966, 1968, 1977; Benović, 1973, 1976; Bender & Benović, 1986; Benović & Bender, 1987; Gamulin & Kršinić, 1993a,b, 2000; Benović & Lučić, 1996, 2001; Batistić *et al.*, 2004; Benović *et al.*, 2005, Lučić *et al.*, 2005, 2009). Comparative analysis of data collected over this period is made easier by the similar sampling methodology used in all studies: that is, vertical tows in several specific layers with standard plankton nets. Although the presentation of results differs from paper to paper, certain useful indicators of system change, such as species composition, relative abundance, and bathymetric distribution, can be extracted from the published data.

Four comprehensive older publications were used in the current analysis: Benović (1976) describes the monthly distribution and abundance of hydromedusae from July 1967 to June 1968; Bender & Benović (1986) and Benović & Bender (1987) evaluate the distribution of medusae based on material collected during seasonal

cruises from 1974 to 1976 at five stations in the deep southern Adriatic; Gamulin & Kršinić (2000) consolidate older data on calycophore siphonophores in the Adriatic Sea based on monthly sampling from July 1967 to June 1968, seasonal cruises from 1974 to 1976, and five cruises from 1993 to 1995.

Similar but more recent investigations began again in 2002 for the international cooperative project "Medusa", summarized by Benović *et al.* (2005) and Lučić *et al.* (2005) who described the bathymetric distribution of medusae and calycophoran siphonophorae during spring 2002, and Lučić *et al.* (2009) who reported on diel vertical migrations of medusae in July 2003. This review compares historical and recent data on cnidarians from the deep southern Adriatic, with unpublished data from February and October 2004 incorporated into the analysis.

MATERIAL AND METHODS

Study area

The Southern Adriatic Sea is a semicircular oligotrophic basin with depths to about 1200 m (Fig. 1). It is confluent with the Eastern Mediterranean Sea via inflow of Ionian Surface Water and Levantine Intermediate Water through the Strait of Otranto (~ 800 m depth), and

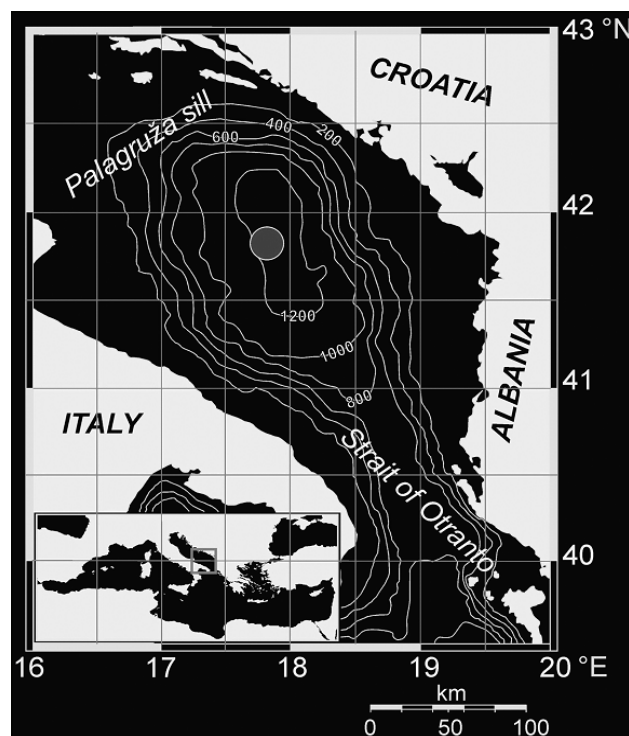


Fig. 1: Location of sampling in the southern Adriatic.
Sl. 1: Lokacija vzorčenja v južnem Jadranu.

with other regions of the Adriatic Sea via currents moving along the Adriatic coast. The region is a source of deep-water that participates in the broader circulation of the Mediterranean Sea (Vilibić & Orlić, 2001) and also features a cyclonic gyre that is present throughout the year (Gačić *et al.*, 2002). Each water mass has a characteristic species assemblage, and the above circulation patterns therefore play an important role in the spatial and seasonal distribution of small zooplankton of the southern Adriatic (Kršinić & Grbec, 2006).

The thermocline starts to form in May and is well developed at 14 m by July or August (Morović *et al.*, 2006). In the deepest layers, temperature is rather constant (from 13 to 15 °C) during the whole year. Salinity is generally higher than 38 throughout the water column (Morović *et al.*, 2006). In September and October, the thermocline is still relatively shallow, at 40 m. As in other parts of the Mediterranean, the thermocline disappears completely in late autumn and winter owing to vertical mixing driven by strong winds.

Whereas temperature changes in the upper 100 m are easily traced to seasonal influences of the local climate, those in deep layers are governed by inter-annual variations in circulation caused by larger-scale pressure differences (Grbec *et al.*, 2009). The deep Mediterranean water that passes through the Strait of Otranto is relatively warmer, saltier, and richer in nutrients than the typical southern Adriatic water. Nutrients often enhance planktonic productivity and, precisely phytoplankton blooms linked to these deeper water masses have been observed (Gačić *et al.*, 2002).

Material and methods

All data analyzed in this paper were collected in the deepest area of the southern Adriatic (1000–1200 m depth). Benović (1976) sampled monthly with an Indian Ocean standard closing net (250 µm mesh, 100 cm diameter) at 0–100, 100–200, 200–300, 300–400, 400–

600, and 600–1000 m. Bender & Benović (1986) and Benović & Bender (1987) used the same nets but sampled with vertical hauls from bottom to surface. The same methodologies were used to collect samples for description of calycophorans during the same period (Gamulin & Kršinić, 2000); from 1993–1995 samples were collected at 0–50, 50–100, 100–200, 300–400, 400–600, and 600–1000 m (Tab. 1).

Project "Medusa" used Nansen opening-closing nets (200 µm mesh, 113-cm diameter) within the following layers: 0–50, 50–100, 100–200, 300–400, 400–600, 600–800, 800–1200 m. The most extensive sampling was conducted in July 2003 when nineteen series (152 vertical hauls) were collected. Owing to a strong thermocline at about 15 m, samples were taken from 0–15 m (above the thermocline) and from 15–50 m depth. Benović *et al.* (2005) and Lučić *et al.* (2005, 2009) provide a detailed description of the study area, sampling program, and methodology for spring and summer cruises. The same methodology was used in February and October 2004 (unpubl. data) when six (48 hauls) and three (24 hauls) sample series, respectively, were collected (Tab. 1).

All plankton samples were preserved in 2.5% formalin-sea water solution buffered with CaCO₃. Cnidarians were identified with a stereomicroscope. Results from historical investigations were presented as the total number of specimens (Benović, 1976; Benović & Bender, 1987) or number of individuals per m² (Bender & Benović, 1986; Gamulin & Kršinić, 2000). Medusae and calycophoran nectophores (polygastric only) in the recent work are expressed as the number of individuals per m³ or 10 m³. Because of these differences, historical and recent comparisons are based on relative frequency of occurrence and abundance where relative frequency of occurrence is: r = rare, observed in < 10% samples during the sampling period; f = frequent, observed in 10%–50% samples during the sampling period; vf = very frequent, observed in >50% during the sampling period.

Tab. 1: Historical and recent arrangement of sampling methodology in the Southern Adriatic Sea.

Tab. 1: Pregled pretekle in sedanje metodologije vzorčenja v južnem Jadranskem morju.

Sampling years	Methodology of sampling	Depth layers (m)
1967–1968	Indian Ocean standard closing net, 100 cm diameter, 250 cm long, mesh size 250 µm	100–0, 200–100, 300–200, 400–300, 600–400, 1000–600
1974–1976	Indian Ocean standard closing net, 113 cm diameter, mesh size 250 µm	From bottom to surface
1993–1995	Nansen opening-closing net, 113 cm diameter, 350 cm long, mesh size 250 µm	50–0, 100–50, 200–100, 300–200, 400–300, 600–400, 1000–600
2002–2004	Nansen opening-closing net, 113 cm diameter, 350 cm long, mesh size 200 µm	15–0, 50–15, 100–50, 200–100, 400–200, 600–400, 800–600, 1200–800

RESULTS AND DISCUSSION

Medusan frequency of occurrence

Most of the 55 medusan species that have been identified in the Adriatic Sea (Benović & Lučić, 1996) have a benthic-pelagic metagenetic life cycle and are carried to the open southern Adriatic with water currents. 18 species of medusae are typical open-ocean holoplanktonic species (Tab. 2), 6 of which were always – or frequently – found in the Adriatic Sea: *Rhabdoon singulare*, *Aglaura hemistoma*, *Persa incolorata*, *Rhopalonema velatum*, *Sminthea eurygaster*, and *Solmissus albescens*. 3 – *Bythotia murrayi*, *Krampella dubia*, and *Haliscera bigelowi* – were rare. The frequency of occurrence of *Solmundella bitentaculata* and *Paraphyllina intermedia* appears to be seasonal. The bathypelagic trachymedusan *Haliscera bigelowi* and the coastal anctomedusan *Dicodinium adriaticum* were found only in recent investigations (Benović *et al.*, 2005).

Other differences between historical and recent data are worthy of note. For example, *Liriope tetraphylla*, tra-

ditionally among the most frequently encountered hydromedusae in this region, was collected only very rarely in recent investigations. In fact, the last time that this medusa was found frequently in samples from the southern Adriatic was November 1993 (Benović & Lučić, 1996). *L. tetraphylla* was observed to undergo large inter-annual variations in abundance and seasonality in the northwestern Mediterranean Sea, but these variations do not appear to be linked to long-term changes in hydrographic conditions (Buecher *et al.*, 1997). There was, however, an inverse relationship between the numbers of *L. tetraphylla* and the scyphomedusa *Pelagia noctiluca* (Buecher *et al.*, 1997). A mass occurrence of *P. noctiluca* observed in the Adriatic from 1997 to 2006 (unpubl. data) coincided with a drastic decrease of *L. tetraphylla* abundance. *Oceania armata*, *Amphinema rubra*, *Leuckartiara octona*, *Octophialucium funerarium*, and *Arctopodema australis* are now found more frequently than in previous investigations and may be considered characteristic of the open southern Adriatic. *Rhopalonema funerarium*, on the other hand, has been found only in recent investigations.

Tab. 2: List of typical Southern Adriatic Sea medusae collected from 1967 to 2004 and their relative frequency of occurrence: r = rare; f = frequent; vf = very frequent. Data sources: 1967–1968, Benović (1976); 1974–1976, Bender & Benović (1986) and Benović & Bender (1987); May 2002, Benović *et al.* (2005); July 2003, Lučić *et al.* (2009); February and October 2004, unpubl.

Tab. 2: Seznam tipičnih meduz južnega Jadranskega morja, zbranih od 1967 do 2004 in relativna pogostost njihovega pojavljanja: r = redko; f = pogosto; vf = zelo pogosto. Podatkovni viri: 1967–1968, Benović (1976); 1974–1976, Bender & Benović (1986) in Benović & Bender (1987); maj 2002, Benović *et al.* (2005); julij 2003, Lučić *et al.* (2009); februar in oktober 2004, neobjavljeno.

Species	1967–1968	1974–1976	May 2002	July 2003	Feb 2004	Oct 2004
<i>Rhabdoon singulare</i>	vf	vf	vf	vf	vf	f
<i>Oceania armata</i>		r	f	f	f	r
<i>Amphinema rubra</i>		r	vf	vf	vf	f
<i>Leuckartiara octona</i>		r	r	f	f	
<i>Bythotia murrayi</i>	r	r		r		
<i>Krampella dubia</i>		r		r		
<i>Octophialucium funerarium</i>	r	r	r	vf	vf	
<i>Haliscera bigelowi</i>			r	r		
<i>Liriope tetraphylla</i>	vf	vf		r		
<i>Aglaura hemistoma</i>	vf	vf	vf	vf	vf	f
<i>Arctopodema australis</i>		r	f	vf	vf	f
<i>Persa incolorata</i>	vf	vf	vf	vf	vf	vf
<i>Rhopalonema funerarium</i>			r	r	f	r
<i>Rhopalonema velatum</i>	vf	vf	vf	vf	vf	vf
<i>Sminthea eurygaster</i>	vf	f	f	f	f	r
<i>Solmundella bitentaculata</i>	f	vf	f	f	f	
<i>Solmissus albescens</i>	vf	vf	vf	vf	vf	vf
<i>Paraphyllina intermedia</i>			f	f		

One obvious difference between historical and recent data is the presence of coastal species in the surface waters of the open southern Adriatic. Hydromedusae of the genera *Hydractinia*, *Bougainvillia*, *Clytia*, and *Obelia*, previously encountered very frequently, are now found only very rarely. This might be related to the substantial changes in the Anthomedusan and Leptomedusan fauna that have occurred in the northern Adriatic (Benović *et al.*, 1987). Namely, as the majority of these meta-genetic species has disappeared in the north, they are no longer transported along the Italian coast to populate the southern Adriatic fauna (Benović *et al.*, 2000).

Calycophoran frequency of occurrence

23 calycophore species were recorded, all in the southern Adriatic. Except for *Muggiaea kochi* and *M.*

atlantica, all of these species are common to, or exclusively found in, the open sea. Compared with historical data, only the rarely encountered *Rosacea cymbiformis* and *Sulculeolaria quadrivalvis* were not found in the recent work.

Calycophore frequency of occurrence does not differ substantially in historical and recent data (Tab. 3). The southern Adriatic's well-developed cyclonic gyre (Gačić *et al.*, 2002) probably contributes to maintaining a relatively constant composition of the plankton community, including gelatinous taxa. The most common species are *Lensia subtilis*, *L. meteori*, *Eudoxoides spiralis*, *Sphaeronectes gracilis*, and *S. irregularis*, followed by *Hippopodius hippopus*, *Vogtia pentacantha*, *L. conoidea*, *L. fowleri*, *Chelophyes appendiculata*, *Kephyes ovata*, and *Bassia bassensis*. The calycophoran *K. ovata*, previously known as *Clausophyes ovata*, was reclassified by Pugh (2006).

Tab. 3: List of typical Southern Adriatic Sea calycophoran nectophores collected from 1965 to 2004 and their relative frequency of occurrence: r = rare; f = frequent; vf = very frequent. Data sources: 1965–1994, summarized in Gamulin & Kršinić (2000); May 2002, Lučić *et al.* (2005); July 2003, Lučić *et al.* (2009); February and October 2004, unpubl.

Tab. 3: Seznam tipičnih kalikofornih cevkašev južnega Jadranskega morja, zbranih od 1965 do 2004 in relativna pogostost njihovega pojavljanja: r = redko; f = pogosto; vf = zelo pogosto. Podatkovni viri: 1965–1994, povzeto v Gamulin & Kršinić (2000); maj 2002, Lučić *et al.* (2005); julij 2003, Lučić *et al.* (2009); februar in oktober 2004, neobjavljeno.

Species	1965–1994	May 2002	July 2003	Feb 2004	Oct 2004
<i>Rosacea cymbiformis</i>	r				
<i>Hippopodius hippopus</i>	f	f	r	f	
<i>Vogtia pentacantha</i>	r	r	f	f	r
<i>Sulculeolaria quadrivalvis</i>	r				
<i>Sulculeolaria turgida</i>	r				
<i>Sulculeolaria chuni</i>	r	r	r		
<i>Diphyes dispar</i>	r				
<i>Lensia conoidea</i>	f	f	f	f	r
<i>Lensia multicristata</i>	r	r	r		
<i>Lensia fowleri</i>	r	f	f	f	
<i>Lensia subtilis</i>	vf	vf	vf	vf	vf
<i>Lensia campanella</i>	r	r	r		
<i>Lensia meteori</i>	vf	vf	vf	vf	vf
<i>Lensia subtiloides</i>	r		r		
<i>Chelophyes appendiculata</i>	f	r	r	f	f
<i>Eudoxoides spiralis</i>	vf	vf	vf	f	vf
<i>Sphaeronectes gracilis</i>	f	vf	vf	vf	
<i>Sphaeronectes irregularis</i>	vf	f	vf	vf	f
<i>Sphaeronectes gamulini</i>	r	r			
<i>Sphaeronectes fragilis</i>	r	r	r		
<i>Kephyes ovata</i>	r	f	f	f	r
<i>Abylopsis tetragona</i>	f	r	r		
<i>Bassia bassensis</i>	f	r	f	f	r

Medusan abundance

These data suggest that important changes have occurred in medusan abundance. Total abundance appears to be higher in recent studies. This is especially the case for *Rhabdoon singulare*, *Oceania armata*, *Octophialucium funerarium*, and *Arctapodema australis*. These species were historically relatively rare, but they are decidedly more abundant and sometimes dominant in our more recent samples (Tab. 4). On the other hand, *Liriope tetraphylla*, previously one of the more numerous medusae, has undergone a dramatic decrease, and in some cases it was absent altogether. *Aglaura hemistoma*, *Persa incolorata*, *Rhopalonema velatum*, and *Solmissus albescens*, however, have remained regularly abundant.

The massive appearance of meroplanktonic coastal species that occurred seasonally in historical studies has not been observed in our more recent work. Nevertheless, medusan densities above 100 m in May 2002 and July 2003 are among the highest reported for any open-sea environment (see Benović et al., 2005 and Lučić et

al., 2009). For example, particularly high densities of *Rhopalonema velatum* were found in the 50–100 m layer, with 358 ind. 10 m^{-3} in May 2002, 93 ind. 10 m^{-3} in July 2003, and 51 ind. 10 m^{-3} in February and October 2004.

Calycophoran abundance

There was no detectable change in the abundance of calycophoran species between earlier and recent samples. *Lensia subtilis* continues to be the most numerous species, followed by *Eudoxoides spiralis* and *L. meteori*. *Sphaeronectes gracilis* and *S. irregularis* also were abundant.

Several species do, however, appear at notably higher abundance in recent investigations (Tab. 5). In particular, *Kephyes ovata* was more numerous; in July 2003, there was an unusually high number of *Vogtia pentacantha*. Further, one of the highest nectophore densities yet reported for the open sea (275 nectophores 10 m^{-3}) was found above 50 m at night in May 2002, due primarily to *L. subtilis* (Lučić et al., 2005).

Tab. 4: Relative abundance of Southern Adriatic Sea medusae collected from 1967 to 2004. Historical data were recalculated as number of individuals per 10 m^3 : + = <1 ind. 10 m^3 ; c = 1–5 ind. 10 m^3 ; cc = >5–10 ind. 10 m^3 ; ccc = >10 ind. 10 m^3 . Data sources: 1967–1968, Benović (1976); 1974–1976, Bender & Benović (1986) and Benović & Bender (1987); May 2002, Benović et al. (2005); July 2003, Lučić et al. (2009); February and October 2004, unpubl.

Tab. 4: Relativna številčnost meduz južnega Jadranskega morja, zbranih od 1967 do 2004. Podatki iz preteklih študij so bili preračunani na število osebkov na 10 m^3 : + = <1 ind. 10 m^3 ; c = 1–5 ind. 10 m^3 ; cc = >5–10 ind. 10 m^3 ; ccc = >10 ind. 10 m^3 . Podatkovni viri: 1967–1968, Benović (1976); 1974–1976, Bender & Benović (1986) in Benović & Bender (1987); maj 2002, Benović et al. (2005); julij 2003, Lučić et al. (2009); februar in oktober 2004, neobjavljeno.

Species	1967–1968	1974–1976	May 2002	July 2003	Feb 2004	Oct 2004
<i>Rhabdoon singulare</i>	c	c	ccc	ccc	c	c
<i>Oceania armata</i>		+	c	c	cc	c
<i>Amphinema rubra</i>		+	c	cc	c	+
<i>Leuckartiara octona</i>		+	+	c	+	
<i>Bythotiara murrayi</i>	+	+		+		
<i>Krampella dubia</i>		+		+		
<i>Octophialucium funerarium</i>	+	+	+	c	c	
<i>Haliscera bigelowi</i>			+	+		
<i>Liriope tetraphylla</i>	ccc	ccc		+		
<i>Aglaura hemistoma</i>	ccc	ccc	c	ccc	ccc	c
<i>Arctapodema australis</i>		+	+	c	c	+
<i>Persa incolorata</i>	ccc	cc	cc	cc	ccc	c
<i>Rhopalonema funerarium</i>			+	+	+	+
<i>Rhopalonema velatum</i>	ccc	ccc	ccc	ccc	ccc	ccc
<i>Sminthea eurygaster</i>	cc	+	c	c	+	+
<i>Solmundella bitentaculata</i>	+	cc	c	c	c	
<i>Solmissus albescens</i>	cc	c	cc	ccc	ccc	c
<i>Paraphyllina intermedia</i>			+	+		

Tab. 5: Relative abundance of Southern Adriatic Sea calycophoran nectophores collected from 1965 to 2004. Historical data were recalculated as number of nectophores per 10 m³: + = <1 ind. 10 m³; c = 1–5 ind. 10 m³; cc = >5–10 ind. 10 m³; ccc = >10 ind. 10 m³. Data sources: 1965–1994, summarized in Gamulin & Kršinić (2000); May 2002, Lučić *et al.* (2005); July 2003, Lučić *et al.* (2009); February and October 2004, unpubl.

Tab. 5: Relativna številčnost kalikoformnih cevkašev južnega Jadranskega morja, zbranih od 1965 do 2004. Podatki iz preteklih študij so bili preračunani na število nektoforov na 10 m³: + = <1 ind. 10 m³; c = 1–5 ind. 10 m³; cc = >5–10 ind. 10 m³; ccc = >10 ind. 10 m³. Podatkovni viri: 1965–1994, povzeto v Gamulin & Kršinić (2000); maj 2002, Lučić *et al.* (2005); julij 2003, Lučić *et al.* (2009); februar in oktober 2004, neobjavljeno.

Species	1965–1994	May 2002	July 2003	Feb 2004	Oct 2004
<i>Rosacea cymbiformis</i>	+				
<i>Hippopodius hippopus</i>	c	c	+	c	
<i>Vogtia pentacantha</i>	+	+	cc	+	+
<i>Sulculeolaria quadrivalvis</i>	+				
<i>Sulculeolaria turgida</i>	+				
<i>Sulculeolaria chuni</i>	+	+	+		
<i>Diphyes dispar</i>	+				
<i>Lensia conoidea</i>	+	c	c	+	+
<i>Lensia multicristata</i>	+	+	+		
<i>Lensia fowleri</i>	+	+	c	+	
<i>Lensia subtilis</i>	ccc	ccc	ccc	ccc	ccc
<i>Lensia campanella</i>	+	+	+		
<i>Lensia meteori</i>	ccc	ccc	ccc	ccc	ccc
<i>Lensia subtiloides</i>	+		+		
<i>Chelophyes appendiculata</i>	c	+	+	c	c
<i>Eudoxoides spiralis</i>	cc	ccc	ccc	c	ccc
<i>Sphaeronectes gracilis</i>	c	ccc	ccc	cc	
<i>Sphaeronectes irregularis</i>	cc	c	cc	cc	c
<i>Sphaeronectes gamulini</i>	+	+			
<i>Sphaeronectes fragilis</i>	+	+	+		
<i>Kephyes ovata</i>	+	c	c	c	+
<i>Abylopsis tetragona</i>	c	+	+		
<i>Bassia bassensis</i>	c	+	c	c	+

There are several potential explanations for the increased abundance of planktonic cnidarians in recent samples:

- Higher average water temperatures than in previous years (Gačić *et al.*, 2006) could have stimulated an increase in general plankton production. Accordingly, recent investigations found particularly high micro- and mesozooplankton densities (except in October 2004, when the total number of cnidarians was low).
- Unlike previously, our recent investigations emphasized day-night sampling, with higher densities near the surface at night.
- The short-term, repetitive sampling used in our recent work provides a more thorough temporal coverage of the study area and so it can be expected to characterize abundance more reliably and also capture less abundant components.

Medusan bathymetric distribution and vertical migration

As noted above, full understanding of the role of planktonic cnidarians in pelagic food webs requires knowledge of bathymetric distribution and migration patterns. Of many factors proposed to explain vertical migratory behavior, most attention was given to light intensity, hydrographic variables, feeding, and predator avoidance. Medusan vertical distributions and migration in the southern Adriatic have been described in recent papers (see Lučić *et al.*, 2009), except for *Solmissus albescens* (Benović, 1973). Table 6 summarizes these data.

Tab. 6: Seasonal bathymetric distribution of typical Southern Adriatic Sea medusae. Data sources only from recent investigations (2002–2004).**Tab. 6: Sezonska batimetrijska distribucija tipičnih meduz južnega Jadranskega morja. Podatkovni viri: samo novejšje raziskave (2002–2004).**

Species	Winter	Spring	Summer	Autumn
<i>Rhabdoon singulare</i>	0–200	50–600	15–600	50–200
<i>Oceania armata</i>	0–100	0–600	15–200	30–400
<i>Amphinema rubra</i>	15–400	100–600	100–800	100–200
<i>Leuckartiara octona</i>		50–400	50–600	
<i>Bythotia murrayi</i>			200–400	
<i>Krampella dubia</i>			400–600	
<i>Octopialucium funerarium</i>	400–1200	200–800	200–1200	
<i>Haliscera bigelowi</i>		600–800	600–800	
<i>Liriope tetraphylla</i>		0–100	0–15	
<i>Aglaura hemistoma</i>	0–100	0–100	0–100	0–30
<i>Arctapodema australis</i>	200–1200	200–800	200–1200	400–800
<i>Persa incolorata</i>	0–1200	100–800	50–1200	0–600
<i>Rhopalonema funerarium</i>	400–1200	200–600	600–800	400–1200
<i>Rhopalonema velatum</i>	0–600	0–1200	0–800	0–600
<i>Sminthea eurygaster</i>	50–400	50–600	100–1200	
<i>Solmundella bitentaculata</i>	0–200	0–400	15–400	
<i>Solmissus albescens</i>	0–1200	0–1200	15–1200	50–1200
<i>Paraphyllina intermedia</i>		600–1200	400–1200	

The only pelagic cnidarian found exclusively above 100 m was *Aglaura hemistoma*, an omnivore that feeds on microphytoplankton and protists (Colin *et al.*, 2003). Most *A. hemistoma* occur quite near the surface, except during summer months when it aggregates just above the thermocline. *Liriope tetraphylla* is also a surface species.

Rhopalonema velatum, *Rhabdoon singulare*, and *Oceania armata* are sub-surface species found mainly above 100 m. These medusae rarely breached the thermocline, but during winter months they were sometimes abundant near the surface at night. Part of the *R. velatum* and *R. singulare* populations, however, sought deeper layers at night.

The more frequent and abundant medusae are characteristic members of the southern Adriatic's upper mesopelagic fauna. These are: *Amphinema rubra*, *Persa incolorata*, *Leuckartiara octona*, *Sminthea eurygaster*, and *Solmundella bitentaculata*, as well as the rare species *Bythotia murrayi*. The highest frequency of occurrence and population density of these species is between 100 and 400 m. A common behavioral feature of this group is that they migrate in both directions at night, that is, both toward the surface and toward the bottom. Their vertical movements are also seasonal, such that in winter these species swim to the surface at night whereas at

other times of the year they do not migrate shallower than 100 m depth.

Characteristic species of the lower mesopelagic are *Octopialucium funerarium*, *Arctapodema australis*, *Rhopalonema velatum*, and a very rare *Krampella dubia*. These species undergo extensive vertical migrations, with their upper border being 200 m.

The scyphomedusa *Paraphyllina intermedia* is mostly bathypelagic and migrates to within 400 m of the surface at night.

The most important vertical migrant is *Solmissus albescens*, behaviorally distinguished from all other species: it has the widest vertical distribution and undertakes the most extensive diel migration, spanning more than 800 m at the average speed of 222 m/h (K. Katja Yong, *pers. comm.*). It aggregates within 400–800 m layer at midday and toward evening moves to upper layers. The highest abundance was found at night between the surface and 50 m. An exception to this pattern occurs in summer and autumn when its upward movement is blocked by a well-developed thermocline. *S. albescens* primarily eats other gelatinous organisms (Raskoff, 2002). Thus, its extensive migrations to surface layers might be explained by appreciably higher densities of their potential prey above 100 m at night.

Calycophoran bathymetric distribution and vertical migrations

There was substantial variation in the depth range of most common calycophorans (Tab. 7): *Lensia conoidea* (100–1200), *L. meteori* (100–1200), *L. subtilis* (0–600), *Sphaeronectes irregularis* (0–600), *L. fowleri* (100–600), *Kephyes ovata* (800–1200), and *Sphaeronectes gracilis* (0–200).

The species distributed mainly above 100 m depth were *Hippopodius hippopus*, *Lensia subtilis*, *L. campanula*, *Chelophyes appendiculata*, *Eudoxoides spiralis*, *Sphaeronectes gracilis*, *S. irregularis*, *S. gamulini*, and *Bassia bassensis*. Typical nocturnal movements toward the surface were recorded only for *L. subtilis* and *Sphaeronectes gracilis*, both of which aggregated below the thermocline during summer. *E. spiralis* migrated both toward the surface and below 100 m.

Calycophores found mainly below 100 m depth were *Sulculeolaria chuni*, *Lensia multicristata*, *L. fowleri*, *L. meteori*, *L. subtiloides*, and *Sphaeronectes fragilis*. These species migrated to shallower layers primarily in winter, except for *L. meteori*, which was collected near the surface. Most specimens of *L. conoidea* and *Vogtia penthacantha* were collected below 400 m during the

day but were as shallow as 100 m at night. *K. ovata* appears to be non-migratory.

There are some differences between historical (Gamulin & Kršinić, 2000) and recent data regarding the maximum depth of some calycophores. In particular, *V. penthacantha* was described earlier as a typical deep-sea species, but our recent collections show that it is routinely found as shallow as 100 m at night. These seeming historical differences are clearly a function of nighttime samples that characterize our more recent field work. Additionally, the maximum depth earlier reported for *Hippopodius hippopus*, *Lensia subtilis*, *L. campanula*, and *Chelophyes appendiculata* was 1000 m, but this is not substantiated by recent investigations.

CONCLUSIONS

The present work reports historical and recent data on the species composition, abundance, bathymetric distribution, and vertical migrations of planktonic cnidarians in the water column over the deepest area of the oligotrophic South Adriatic Sea. 11 species were found on all cruises, with the more abundant being medusa *Rhopalonema velatum* and the siphonophore *Lensia subtilis*.

Tab. 7: Seasonal bathymetric distribution of typical Southern Adriatic Sea open-sea calycophores. Data sources from recent investigations (2002–2004).

Tab. 7: Sezonska batimetrijska distribucija tipičnih, v odprtih vodah južnega Jadranskega morja živečih kalikoformnih cevkašev. Podatkovni viri: novejša raziskave (2002–2004).

Species	Winter	Spring	Summer	Autumn
<i>Hippopodius hippopus</i>	0–200	0–100	0–200	
<i>Vogtia penthacantha</i>	0–800	100–200	200–1200	400–600
<i>Sulculeolaria chuni</i>		100–400	0–200	
<i>Lensia conoidea</i>	100–1200	400–1200	100–1200	400–600
<i>Lensia multicristata</i>		100–400	100–400	
<i>Lensia fowleri</i>	50–400	100–400	100–600	
<i>Lensia subtilis</i>	0–600	0–200	0–600	0–200
<i>Lensia campanella</i>		50–100	50–400	
<i>Lensia meteori</i>	0–400	50–800	100–600	200–600
<i>Lensia subtiloides</i>			100–600	
<i>Chelophyes appendiculata</i>	0–200	0–100	15–50	200–600
<i>Eudoxoides spiralis</i>	0–200	0–300	0–1200	0–800
<i>Sphaeronectes gracilis</i>	0–200	0–400	0–200	
<i>Sphaeronectes irregularis</i>	0–600	50–200	15–600	50–400
<i>Sphaeronectes gamulini</i>		50–100		
<i>Sphaeronectes fragilis</i>		100–400	15–800	
<i>Kephyes ovata</i>	600–1200	600–1200	600–1200	
<i>Abylopsis tetragona</i>		100–400	0–50	
<i>Bassia bassensis</i>	0–100	0–100	0–200	0–50

Liriope tetraphylla, formerly among the most frequently encountered hydromedusae in the southern Adriatic, has become rare or absent in recent samples. On the other hand, *Oceania armata*, *Amphinema rubra*, *Leuckartiara octona*, *Octophialucium funerarium*, and *Arctopodema australis*, are now far more abundant than before. These 5 species are now quite common members of the open southern Adriatic planktonic ecosystem. With the exception of *O. armata*, all of these species are characteristic of mid-depth and bathypelagic layers.

One obvious difference between historical and recent collections is the presence of coastal species in the surface waters of the open southern Adriatic. Hydromedusae of the genera *Hydractinia*, *Bougainvillia*, *Clytia*, and *Obelia* that were frequently encountered in our older zooplankton samples are now quite rare. There is, however, no substantial difference in the frequency of occurrence of calyphores between historical and recent samples.

There is, nonetheless, an indication that cnidarians are generally more abundant in our more recently collected samples. This is especially the case for *Rhabdoon singulare*, *Oceania armata*, *Octophialucium funerarium*, and *Arctopodema australis*, species that were previously present only in low abundance and are now more

abundant or, in some cases, even dominant. Higher abundances were recorded for other species during recent investigations, too. This could be explained by the increase of average temperature in the last decade and its influence on the general increase of plankton abundance, or it may be a sampling artifact associated with more frequent sampling at night.

The most common species migrated over a substantial depth range, presumably due to daily changes of irradiance and feeding biology. Higher surface layers temperature appeared to be an effective upper barrier for many cnidarians, especially mesopelagic species. Some populations performed migrations that appeared to track light intensity preference. Certain species also characterize given depth ranges. Long-term sampling programs are critical for an understanding of the planktonic species assemblages in the water column.

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PLANKTONSKI OŽIGALKARJI V ODPRTIH VODAH JUŽNEGA JADRANSKEGA MORJA: PRIMERJAVA PODATKOV IZ PRETEKLIH IN NOVEJŠIH RAZISKAV

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POVZETEK

V pričujočem članku avtorji primerjajo podatke iz preteklih (1967–68, 1974–1976, 1993–1995) in novejših raziskav (2002–2004), in sicer o zgradbi, številčnosti, batimetrijski distribuciji in vertikalni migraciji ožigalkarjev v globokih vodah južnega Jadrana. 18 vrst meduz je tipičnih holoplantonskih vrst, živečih v odprtih morjih; vzorci so vedno ali pogosto vsebovali 6 od teh, in sicer *Rhabdoon singulare*, *Aglaure hemistoma*, *Persa incolorata*, *Rhopalomena velatum*, *Sminthea eurygaster* in *Solmissus albescens*. Najpogostejši kalikoformni cevkaši so *Lensia subtilis*, L.

meteori, *Eudoxoides spiralis*, *Sphaeronectes gracilis* in *S. irregularis* ter *Hippopodius hippopus*, *Vogtia penthacantha*, *Lensia conoidea*, *L. fowleri*, *Chelophyes appendiculata*, *Kephyes ovata* in *Bassia bassensis*. *Pri primerjanju podatkov iz preteklih in novjših raziskav so bile ugotovljene nekatere razlike v prisotnosti in številčnosti.*

Ključne besede: južno Jadransko morje, meduze, kalikoformni cevkaši, zgradba, številčnost, batimetrijska distribucija

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Review article
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FISH AND JELLYFISH: USING THE ISOLATED MARINE 'LAKES' OF MLJET ISLAND, CROATIA, TO EXPLORE LARGER MARINE ECOSYSTEM COMPLEXITIES AND ECOSYSTEM-BASED MANAGEMENT APPROACHES

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ABSTRACT

The marine 'lakes' of Mljet Island, southern Croatia, provide an interesting ecological setting for investigating structure and function of marine ecosystems outside the lakes. This paper synthesizes some of the historical and ongoing research projects involving the lakes, with special attention given to recent studies on the isolated lake population of the scyphozoan Aurelia sp. 5. This species appears to be geographically isolated within and evolutionarily limited to the lakes of Mljet Island. As such, we are utilizing the lakes as a tool to better understand the ecological relationship between jellyfish and a diverse community of fish species that also inhabit the lakes. We promote future studies to parameterize an ecosystem model of the lakes as a test-bed system for an ecosystem-based management approach using similar models outside the lakes.

Key words: medusae, planktivorous fishes, *Aurelia*, *Boops*, *Atherina*

PESCI E MEDUSE: UTILIZZO DEI 'LAGHI' MARINI ISOLATI DELL'ISOLA DI MLJET, CROAZIA, PER LO STUDIO DELLE COMPLESSITÀ DI UN PIÙ AMPIO ECOSISTEMA MARINO E APPROCCI PER UNA GESTIONE BASATA SUGLI ECOSISTEMI

SINTESI

I 'laghi' marini dell'isola di Mljet, Croazia meridionale, forniscono un interessante ambito ecologico per lo studio della struttura e della funzione degli ecosistemi marini esterni ai laghi. L'articolo sintetizza alcuni dei progetti di ricerca storici e attuali che coinvolgono i laghi, con una speciale attenzione rivolta a studi recenti sulle popolazioni di scifozoi Aurelia sp. 5. Tale specie risulta essere geograficamente isolata ed evolutivamente limitata ai laghi dell'isola di Mljet. I laghi vengono quindi utilizzati quali strumenti per una migliore comprensione delle relazioni ecologiche fra le meduse e diverse comunità di pesci, che pure vivono nei laghi. Gli autori incoraggiano future ricerche finalizzate a parametrizzare un modello ecosistemico dei laghi, che possa servire quale sistema sperimentale di approccio per una gestione basata sugli ecosistemi, che si avvalga pure di modelli simili esterni ai laghi.

Parole chiave: meduse, pesci planctivori, *Aurelia*, *Boops*, *Atherina*

INTRODUCTION AND BACKGROUND

Geographically isolated marine lakes and lagoons are particularly intriguing for marine scientists as they provide opportunities to understand population, community or ecosystem-level processes without compounding effects of immigration and emigration. While evolutionary biologists realize opportunities to study rates of speciation under restricted gene flow (e.g., Dawson & Hamner, 2005), community and ecosystem ecologists can investigate underlying processes that regulate population numbers and the flow of energy and nutrients within the system (Hamner *et al.*, 1982; Schneider & Behrends 1998; Malej *et al.*, 2007). Importantly, ecosystem models such as those employed to manage marine fisheries (Christensen & Walters, 2004) can be developed and refined from isolated marine lake and lagoon ecosystems. These nearly-enclosed systems act in essence as large, natural laboratories to explore fully the ecological complexities (e.g., competition and predation) of important open systems that are otherwise intractable for study.

The lakes of Mljet Island, Croatia, are particularly interesting as they contain a seemingly resident and

quasi-stable population of medusae embedded within a diverse community of nektonic, demersal and benthic organisms (Vučetić, 1961; Benović *et al.*, 2000; Peharda *et al.*, 2002). To this end, a multi-national group of marine scientists has been studying the ecology and hydrographic setting of the marine 'lakes' of northern Mljet Island, Croatia, as part of Project 'Meduza'. This paper describes this isolated marine setting, its natural history and the scientific benefit of using the Mljet lakes as model ecosystems to explore ecosystem-based management strategies beyond the lakes with special attention given to the role of jellyfish (e.g., *Aurelia* sp. 5; Dawson & Jacobs, 2001) in marine ecosystem structure and function.

GEOLOGICAL HISTORY OF MLJET ISLAND'S 'LAKES'

The geological history of the Mljet Island doline marine system is a complex result of the porous carbonate terrain, subterranean aquifers, and eustatic sea level rise over the past 10,000 years. The entirety of the Dalmatian coast is comprised of thousands of islands as a result of both tectonic lifting followed by late Pleistocene-Holocene flooding of the coastal region (Wunsam *et al.*,

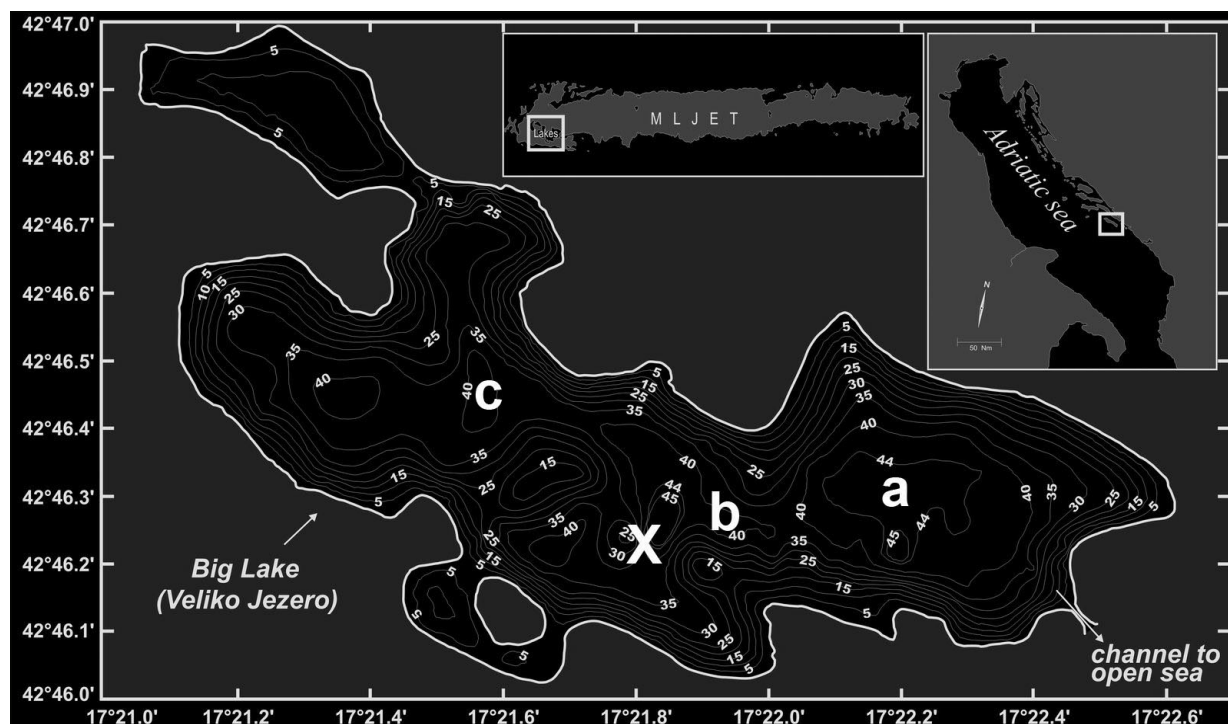


Fig. 1: Bathymetric map of Veliko Jezero on the northern end of Mljet Island, Croatia, in the southern Adriatic Sea. The two basins marked (a, b) are the location of a resident population, though medusae also make excursions into the basin labeled as (c). Location of outcroppings where polyps are located is indicated by the (x).

Sl. 1: Batimetrična karta Velikega jezera na severnem koncu otoka Mljeta, Hrvatska, južno Jadransko morje. Kotanji označeni z (a, b) sta lokaciji rezidentne populacije, čeprav se meduze pojavljajo tudi v kotanji označeni s (c). Lokacija polipov je označena z (x).

1999). Dominating the karstic landscape of the northern end of Mljet Island are several depressions. The modern expression of these depressions includes two fjord-like marine 'lakes', Malo Jezero (MJ) (Small Lake) and Veliko Jezero (VJ) (Big Lake). The term 'lake' here is a misnomer as there is connectivity of Veliko Jezero to the outer sea via the shallow and long Soline Channel (SC) (Fig. 1). It is believed that the smaller of the two lakes, Malo Jezero, with a maximum depth of ~35 m, is fed by subaquatic springs and was essentially a freshwater lake until a small channel (~1 m deep by 2 m wide by 29 m long) was opened in the 13th Century by resident Benedictine monks to allow small vessel passage from VJ into MJ (Wunsum *et al.*, 1999). Small daily exchange of surface water between the outer Adriatic Sea and VJ through the SC, as well as between the two lakes, is tidally driven.

Veliko Jezero is a series of three basins separated by sills (Fig. 1) that allow surface-water exchange but not deep-water exchange. The southeastern-most basin of VJ has a maximal depth of 46 m and has the most direct connection to the outer Adriatic Sea via SC through a naturally occurring passage. Exchange of water and animals including medusae between basins may occur during rare excursions into the surface layer where residual tidal or wind driven flows forces lateral advection into adjacent basins (Benović *et al.*, 2000). The historical depth of the sill into VJ was about 0.6 m, but this was increased to its current depth of ~2.5 m by the Yugoslav navy in the 1950s to allow deeper draft vessels into the lakes (Benović *et al.*, 2000).

RESIDENCY OF LAKE *AURELIA* SP.: RECENT INVASION OR HOLOCENE RELICT?

Using diatom assemblage and geochemical mineral analysis of cores from the Mljet lakes, Wunsum *et al.* (1999) suggested that VJ began filling with seawater via percolation about 8,400 ybp, and true seawater ingress through SC did not occur until about 5,000 ybp. Suric *et al.* (2005) dated marine encrustations on speleothems from a submarine cave north of Mljet to suggest sea level reached -3 m about 4,000 ybp. Therefore, we can reasonably place a range of at least 4,000 ybp and not greater than 5,000 ybp as the period when an open connection between VJ and the Adriatic occurred (*i.e.*, the earliest period of potential colonization by *Aurelia* sp. in the lakes).

A variety of evidence supports an emerging theory that *Aurelia* sp. 5 is a locally retained relict population from a Mediterranean cold-water phase several thousand years ago. Two key molecular studies by Dawson & Jacobs (2001) and Schroth *et al.* (2002) independently showed marked divergence from other *Aurelia* populations found in the Adriatic and Mediterranean Seas. Interestingly, Schroth *et al.* (2002) placed Mljet medusae

within a boreal clade of *Aurelia* closely related to individuals sampled from the North Atlantic, which could account for the cold-water affinity of Mljet *Aurelia*. Endemism and local adaptation of jellyfish in marine lakes is not novel and has been described previously in tropical settings like marine lakes and lagoons of Palau, western Pacific (Hamner & Hauray, 1981; Hamner *et al.*, 1982; Dawson & Hamner, 2005).

Timing the establishment of *Aurelia* in the lakes is difficult, but there were two major cooling episodes in the southern Adriatic Sea during the Holocene (Sangiorgi *et al.*, 2003). Approximately 7,000 ybp, winter temperatures were decreased on average by about 2 °C, and 3,000 ybp when spring (and possibly summer) temperatures were lowered on average by about 3 °C. The former cooling predates the opening of the lakes to direct exchange, but the latter cooling period 3,000 ybp was after the opening of SC to the Adriatic Sea. We believe local retention and isolation is facilitated by medusa behavior and physiology in response to the unique local hydrography (see, Graham *et al.*, 2001 for a review) that maintains adequate thermal regime (<15 °C year-round) within the lakes (Benović *et al.*, 2000) that is reminiscent of this Holocene cold-water phase.

REGULATION OF FISH POPULATIONS IN THE MLJET LAKES

Using readily available database information (Fish-Base Project, <http://www.fishbase.org>) and historical observations by us (Onofri, *unpubl. data*), we compiled a list of 53 species and 2 genera believed to occur within the Mljet lakes (Tab. 1). This list certainly contains several transient migratory species (*e.g.*, *Sphyma mokarran* and *Scorpaenidae* spp.), but the majority tends to be either reef or seagrass (*Posidonia oceanica*) associated species. Only 5 species, *Atherina boyeri*, *Spicara maena*, *Liza aurata*, *Boops boops* and *Spondyllosoma cantharus*, are described as zooplanktivorous at the adult stage (www.fishbase.org) with the rest preying largely on zoobenthos or larger invertebrate prey with the exception of *Sarpa salpa* which is herbivorous. Of these zooplanktivores, *Atherina*, *Liza* and *Boops* have calculated trophic levels that are similar to the trophic levels calculated previously for *Aurelia* spp. elsewhere (Pauly *et al.*, 2009). This latter point is relevant to our studies because trophic overlap is a key element in discerning resource competition between jellyfish and fish.

With the exception of the transient migrants (sharks and mackerels), the lakes appear to lack higher order predatory fish populations. This is despite the apparent abundance of nocturnally schooling fish believed to be largely comprised of *Boops boops* and *Atherina boyeri* based on our own observations from video and acoustics (Alvarez Colombo *et al.*, 2009; Fig. 2). Thus, with the lack of apparent predation mortality by piscivorous

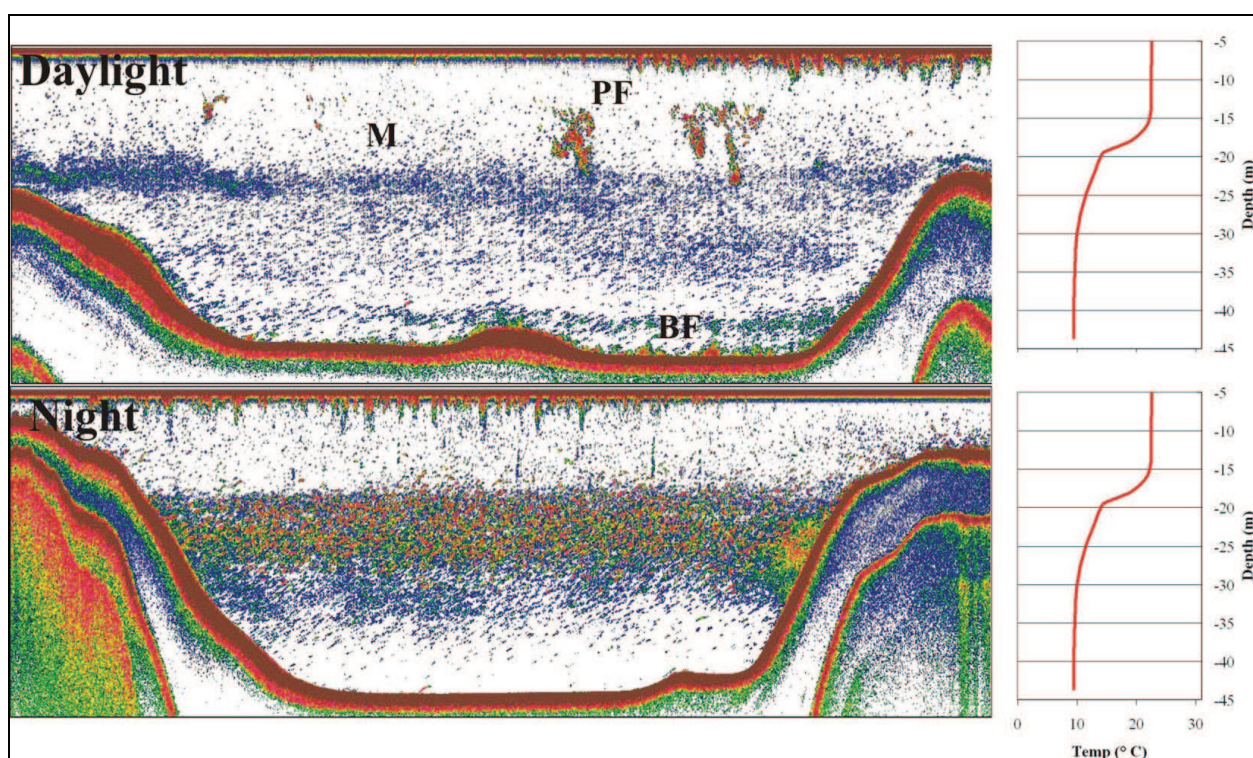


Fig. 2: Acoustic echogram of the southern-most basin in Veliko Jezero at daylight and at night. During the day, jellyfish (labeled M) exclusively occupy the sub-thermocline region, with benthic fishes (BF) below and pelagic schooling fishes (PF) above the medusa layer. At night, medusae and fish occupy the same layer in the water below the thermocline.

Sl. 2: Akustični ehogram najjužnije kotline v Velikem jezeru podnevi in ponoči. Podnevi se meduze (označene z M) nahajajo izključno pod termoklino, pod njimi se gibljejo bentoške ribe (BF), nad njimi pa pelaške ribe v jatah (PF). Ponoči se tako meduze kot ribe gibljejo v istem sloju pod termoklino.

fishes as well as a very minimal artisanal fishery in the protected lakes, we believe population regulation of fish is driven by a combination of bottom-up processes (*i.e.*, productivity) and intra- or inter-specific competition.

Very little information exists on the role of food resource competition involving fish or jellyfish (but see Purcell & Arai, 2001). We suggest inter-specific competition between fish and jellyfish is likely rare unless spatial, temporal and trophic overlap is strong. Moreover, resource partitioning within overlapping resources is likely rare as well, and the expectation is that longer-lived and slower-growing fish are competitively dominant over 'opportunistic' jellyfish unless mortality (either natural or fishing) removes enough fish to force jellyfish into a niche-occupying role. This makes the Mljet lake system particularly interesting because both jellyfish and fish, at least the likely competitors *Atherina*, *Liza*, and *Boops*, overlap in a fashion that seems to promote strong intra-specific competition (see for example Alvarez Colombo *et al.*, 2009 and our Fig. 2). Thus one of the more important continuing research areas is to collect accurate species-specific biomass and trophic information for

both jellyfish and zooplanktivorous fish to realize the extent of competitive interactions that might lead to regulation of fish and jellyfish populations.

REGULATION OF *AURELIA* SP. 5 POPULATIONS IN MLJET'S LAKES

We hypothesize that bottom-up controls are important for the regulation of jellyfish biomass whether they are driven strictly by changes in primary production, detritus delivery or through variations in competition for food resources with planktivorous fishes. We cannot ignore, however, that predation on jellyfish by fish may be an important source of top-down control of *Aurelia* sp. Interestingly, bogue (*Boops boops*) is described as a predator of jellyfish (www.fishbase.org) and we have observed directly the consumption of a tethered *Aurelia* sp. by *Boops boops* during acoustical calibrations in VJ (H. Mianzan and colleagues, *pers. comm.*). A number of examples of medusivory by fishes have been published or reviewed (*e.g.*, Mianzan *et al.*, 2001; Arai, 2005), however, it remains unclear whether such predation con-

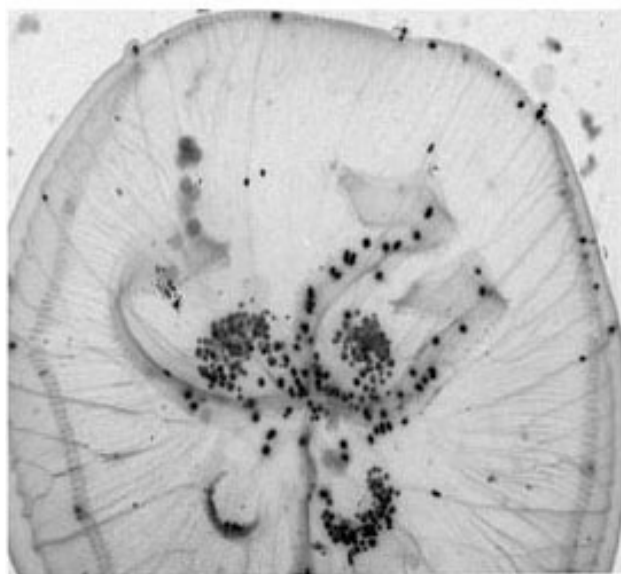


Fig. 3: Heavily parasitized *Aurelia* sp. 5 medusa from Veliko Jezero, Mljet Island. The anthozoan parasites are the numerous reflective points around the oral lobes and semi-circular gonads.

Sl. 3: Močno parazitirana meduza vrste *Aurelia* sp. 5 iz Velikega jezera, otok Mljet. Antozojski paraziti so vidni kot številne odsevne točke okoli ustnih krp in polkrožnih spolnih žlez.

tributes to top-down population regulation of jellyfish in open systems. The Mljet system will hopefully provide insight into such interactions in the future.

Another important source of regulation of *Aurelia* sp. in this system is parasitism. We previously measured parasitic loads of larval anthozoans (Fig. 3), presumably of the genus *Edwardsiella* in the tissues of *Aurelia* sp. 5 in VJ (D'Ambra & Graham, 2009). More than 50% of the population is moderately to heavily parasitized during warmer, stratified periods (Chiaverano & Graham, *unpubl. data*) and parasite loads dropping to around 25% of the population during the unstratified winter period. Chiaverano & Graham (*unpubl. data*) show that parasitism retards growth and alters morphology of *Aurelia* sp. 5 in a way that presumably changes swimming patterns and strength. The alteration of energy transfer away from somatic and reproductive tissue undoubtedly has a large but still unquantified impact on *Aurelia* sp. 5 population dynamics. While parasitic loads tend to be much lower in open marine systems, their influence on populations of jellyfish is relatively unexplored, and the Mljet system may provide insight into parasitism as a potential regulator of nuisance jellyfish blooms elsewhere.

By nature of their bipartite life-histories, the abundance of the medusa stage of *Aurelia* sp. is inextricably linked to the dynamics of the benthic polyp populations.

Thus, any inferences about population dynamics of *Aurelia* sp. 5 in the Mljet lakes must be made in the context of the polyp stage. No published accounts of polyp population dynamics are available, however our own observational work revealed polyps along a narrow band of rocky outcroppings below about 22 m along the northern rim of the southern-most basin of VJ (Fig. 1). Several observational SCUBA dives made during spring, summer and winter found active strobilation (= production of new medusae) during each of these periods. While year-round occurrence of *Aurelia* sp. 5 may be due to longevity and stability of the population, it may also be due to a constant infusion of young medusae throughout the year (Malej *et al.*, 2009). Moreover, constant production of young medusae may be a bet-hedging strategy against pulsed food supplies, thus equalizing the competitive advantage that slower growing, longer-lived fish have over time.

MLJET LAKES AS MODEL ECOSYSTEMS FOR MANAGEMENT

Ecosystem-based approaches are gaining in popularity for the management of marine fisheries (Christensen & Walters, 2004). Because these approaches rely heavily on modeling strategies, their utility for understanding whole system processes is largely limited by quality data to support their development and accuracy. While jellyfish are grossly underrepresented in published ecosystem models (Pauly *et al.*, 2009) there are a few examples demonstrating a key role for jellyfish in ecosystem functioning largely through bottom-up controls on predators (e.g., sea turtles populations) or top-down controls on zooplankton prey (Feigenbaum & Kelly, 1984; Schneider & Behrends, 1998). Inclusion of jellyfish in ecosystem models is limited largely by the lack of adequate time-series data on abundance and by the relatively poor understanding of diet and growth.

We promote the utility of the Mljet lakes system as model marine ecosystem to explore ecosystem-based management approaches using models that accurately reflect the functional role of jellyfish. Critical in the development of accurate ecosystem models are diversity of functional compartments, knowledge of diet and growth parameters, quality time-series information on populations. Also important to fisheries management is the availability of accurate fishery-independent data to support the fishery-dependent assessment of population structure.

The Mljet lakes provide a rare opportunity to develop a functional ecosystem model (e.g., with EwE) using realistic data rather than manipulated approximations. Owing to similarities of species or ecological guilds, such a model would be comparative of ecosystems outside of the lakes. To this end, the Mljet lake system offers high functional and trophic diversity of benthic, demer-

sal, nektonic and planktonic organisms suitable for model development. Interestingly, these small lakes were the subject of whole-lake nutrient enrichment experiments during the 1950s at which time inorganic phosphorus was added in an attempt to stimulate fish and shellfish production (Buljan, 1957; Puchér-Petković, 1960; Vučetić, 1957, 1966). Unfortunately there is little available quantitative information on jellyfish populations in response to increased nutrient loading, but we continue to explore available datasets for more information from these experiments.

The lakes are small and relatively contained allowing the accurate collection of system-wide data on population structure for mobile organisms (specifically fish and jellyfish) without great concern for variations due to immigration and emigration. Most of the target species are either well-represented outside the lakes with complete data on growth and diet (see www.FishBase.org), or we are currently collecting the necessary information in ongoing studies (e.g., *Aurelia* sp.). And finally, owing to the

small size of the lakes and their protection from large-scale fishing, we can carefully assess an ecosystem model with fishery-independent statistics and, by working closely with Mljet residents, we can accurately determine catch statistics for the small artisanal fishery of the lakes.

In conclusion, the lakes of northern Mljet Island, Croatia, are likely unique in their temperate marine setting and geographic isolation. Because of this, we see opportunity to use the lakes as a model ecosystem to test the development and application of ecosystem-based management models with respect to the role of jellyfish as a potentially important component of marine ecosystems. In light of the potential for jellyfish populations to increase under added human stressors (coastal eutrophication, over-harvesting of fish, habitat modification and climate change), we see this opportunity as a critical step for marine scientists and fishery managers to refine their modeling tools to accurately reflect the trophic role of jellyfish at the ecosystem scale.

Tab. 1: Check list of fish species and families found in the marine lakes of Mljet Island, Croatia. Also presented are common and regional names. Information collected from the online resource www.fishbase.org includes relative importance of the species for fishing (- is not fished; + is minor fishing; ++ is moderately fished; +++ is heavily fished), whether the species is a zooplanktivorous (* indicates only early stages known to prey on zooplankton), and trophic level values where 2.0 is entirely herbivorous, 3.0 is a first order carnivore, 4.0 a second order carnivore, and so on.

Tab. 1: Seznam ribjih vrst in družin iz morskih jezer na otoku Mljetu, Hrvatska. Našteta so tudi splošna in regijska imena. Podatki, pridobljeni s spletne strani www.fishbase.org, vključujejo tudi informacijo o pomenu vrste za ribolov (- se ne lovi, + se lovi redko, ++ se lovi zmerno, +++ se veliko lovi), prehranjevanju vrste z zooplanktonom (* označuje samo zgodnje razvojne oblike, ki se hranijo z zooplanktonom) in trofičnih ravneh, in sicer 2.0 za popolnoma rastlinojede vrste, 3.0 za mesojede vrste prvega reda, 4.0 za mesojede vrste drugega reda, itd.

Family	Scientific name	Common name	Regional name	Fishing pressure	Zooplankton feeding	Trophic level
Anguillidae	<i>Anguilla anguilla</i>	European eel	Angulja	++	N	2.3-3.5
Apogonidae	<i>Apogon imberbis</i>	Cardinal fish	Matulicic	+	N	3.9
Atherinidae	<i>Atherina boyeri</i>	Big-scale sand smelt	Brfun	++	Y	2.2-3.1
Belonidae	<i>Belone belone</i>	Garpike	Jagla	++	N	4.0-4.2
Blenniidae	<i>Parablennius</i> spp.			-	N	3.0-3.5
Carangidae	<i>Pseudocaranx dentex</i>	White trevally	Šnjurak	++	Y*	3.1-3.9
Carangidae	<i>Seriola dumerili</i>	Greater amberjack	Bilizmuša	++	N	3.7-4.5
Centranchidae	<i>Spicara maena</i>	Blotched picarel	Cipavica	+	Y	3.0-4.2
Congridae	<i>Conger conger</i>	European conger	Grum	++	N	3.5-4.5

Family	Scientific name	Common name	Regional name	Fishing pressure	Zooplankton feeding	Trophic level
Gadidae	<i>Merlangius merlangus</i>	Whiting	Pišmolj	+++	Y*	3.2-4.5
Gadidae	<i>Trisopterus minutus</i>	Poor cod	Mol	++	N	3.2-4.0
Gobiesocidae	<i>Lepadogaster lepadogaster</i>	Shore clingfish	Priljepnjak kamenjaric	-	N	N/A
Gobiidae	<i>Gobius</i> spp.			-	N	3.0-3.5
Labridae	<i>Coris julis</i>	Mediterranean rainbow wrasse	Dundica	+	N	3.2-3.6
Labridae	<i>Labrus merula</i>	Brown wrasse	Crnac	+	N	3.2-3.5
Labridae	<i>Symphodus cinereus</i>	Grey wrasse	Hinac sivi	+	N	3.2-3.3
Labridae	<i>Symphodus dodonleini</i>		Cucuruša	-	N	N/A
Labridae	<i>Symphodus mediterraneus</i>	Axillary wrasse	Podujka	+	N	3.2
Labridae	<i>Symphodus melops</i>	Corkwing wrasse	Kosirica mjesecica	+	N	3.2
Labridae	<i>Symphodus ocellatus</i>		Martinka	-	N	2.5-3.3
Labridae	<i>Symphodus roissali</i>	Five-spotted wrasse	Kosirica	+	N	3.4-3.5
Labridae	<i>Symphodus rostratus</i>		Dugonosica	-	N	3.3-3.7
Labridae	<i>Symphodus tinca</i>	East Atlantic peacock wrasse	Božjak	+	N	N/A
Mugilidae	<i>Liza aurata</i>	Golden grey mullet	Cipal zlatac	++	Y	2.2-2.9
Mullidae	<i>Mullus barbatus barbatus</i>	Red mullet	Barbun	++	N	2.7-3.6
Mullidae	<i>Mullus surmuletus</i>	Striped red mullet	Barbun	++	N	3.0-3.5
Muraenidae	<i>Muraena helena</i>	Mediterranean moray	Marina	-	N	N/A
Pomacentridae	<i>Chromis chromis</i>	Damselfish	Crnej	+	N	3.0-4.2
Sciaenidae	<i>Sciaena umbra</i>	Brown meagre	Kavala	++	N	3.8
Scombridae	<i>Scomber japonicus</i>	Chub mackerel	Lancarda	+++	Y*	2.8-4.3
Scombridae	<i>Scomber scombrus</i>	Atlantic mackerel	Bokulja	+++	Y*	3.0-4.4
Scorpaenidae	<i>Scorpaena porcus</i>	Black scorpionfish	Bodec	+	N	3.5-4.3
Scorpaenidae	<i>Scorpaena scrofa</i>	Largescalded scorpionfish	Crljenak	++	N	4.2-4.4
Serranidae	<i>Epinephelus caninus</i>	Dogtooth grouper	Kirnja zubuša	++	N	N/A
Serranidae	<i>Epinephelus costae</i>	Goldblotch grouper	Kirnja zatica	+	N	N/A

Family	Scientific name	Common name	Regional name	Fishing pressure	Zooplankton feeding	Trophic level
Serranidae	<i>Epinephelus marginatus</i>	Dusky grouper	Kirnja	+++	N	3.7–4.3
Serranidae	<i>Serranus cabrilla</i>	Comber	Giricar	+	N	3.4–4.4
Serranidae	<i>Serranus hepatus</i>	Brown comber	Cucin	+	N	3.5–3.8
Serranidae	<i>Serranus scriba</i>	Painted comber	Buruca	+	N	3.8
Soleidae	<i>Solea solea</i>	Common sole	List	+++	N	3.0–3.3
Sparidae	<i>Boops boops</i>	Bogue	Batelj	+++	Y	2.5–3.0
Sparidae	<i>Dentex dentex</i>	Common dentex	Dental	++	N	4.5
Sparidae	<i>Diplodus annularis</i>	Annular seabream	Baraj	++	N	3.1–3.4
Sparidae	<i>Diplodus puntazzo</i>	Sharpsnout seabream	Karoc	++	N	2.9
Sparidae	<i>Diplodus vulgaris</i>	Common two-banded seabream	Crnoguz	++	N	3.1–3.8
Sparidae	<i>Lithognathus mormyrus</i>	Striped seabream	Arkaj	+	N	N/A
Sparidae	<i>Oblada melanura</i>	Saddled seabream	Cešalj	++	N	3.0
Sparidae	<i>Pagellus acarne</i>	Axillary seabream	Arbun	++	N	3.3–4.4
Sparidae	<i>Pagellus erythrinus</i>	Common pandora	Arbor	++	Y*	3.2–3.8
Sparidae	<i>Sarpa salpa</i>	Salema	Salpa	++	N	2.0
Sparidae	<i>Spondylusoma cantharus</i>	Black seabream	Grobar	++	Y	3.2–3.3
Synodontidae	<i>Synodus saurus</i>	Atlantic lizardfish	Gušter	+	N	4.5
Trachinidae	<i>Trachinus draco</i>	Greater weever	Dragan	+	N	N/A
Zeidae	<i>Zeus faber</i>	John dory	Kovač	++	Y*	3.7–4.5

RIBE IN MEDUZE: UPORABA IZOLIRANIH MORSKIH 'JEZER' NA OTOKU MLJETU, HRVAŠKA, PRI RAZISKOVANJU KOMPLEKSNOСТИ VEČJEGA MORSKEGA EKOSISTEMA IN PRISTOPOV EKOSISTEMSKEGA UPRAVLJANJA

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POVZETEK

Morski 'jezeri' na otoku Mljetu, južna Hrvaška, predstavljata zanimivo ekološko okolje za raziskovanje strukture in funkcije morskih ekosistemov zunaj samih jezer. Pričujoči članek sintetizira nekatere pretekle in sedanje raziskovalne projekte na jezerih s posebnim poudarkom na novjših študijah izolirane jezerske populacije klobučnjaške meduze *Aurelia* sp. 5. Ta vrsta je po vsej verjetnosti geografsko izolirana in evolucijsko omejena na jezeri otoka Mljeta. Kot taki jezeri predstavljata orodje za boljše razumevanje ekološkega razmerja med meduzami in raznoliko skupnostjo ribjih vrst, ki prav tako naseljujejo jezeri. Z bodočimi študijami avtorji spodbujajo k parametriziranju ekosistemskega modela jezer kot preizkusnega sistema za pristop ekosistemskega upravljanja ter uporabo podobnih modelov zunaj samih jezer.

Ključne besede: meduze, planktivore ribe, *Aurelia*, Boops, *Atherina*

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AURELIA SP. 5 (SCYPHOZOA) POPULATION IN THE MLJET LAKE (THE SOUTHERN ADRIATIC): TROPHIC INTERACTIONS AND LINK TO MICROBIAL FOOD WEB

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ABSTRACT

Vertical distribution, population structure and chemical composition of a population of the scyphomedusan Aurelia sp. 5 were studied in the Mediterranean euhaline lake on Mljet Island (Veliko jezero, the Southern Adriatic) where dense aggregations have been observed throughout the year. A majority of Aurelia were located in a layer below the thermocline with temperatures 13–19 °C over most of the day during summer, whereas in October the population was shallower. The medusae migrated towards the surface at dusk but rarely crossed the thermocline. Elemental analysis of Aurelia revealed low dry weight specific carbon, nitrogen and phosphorus content ranging from 0.9–1.7%, 0.2–0.5% and 0.02–0.06%, respectively. In addition to the direct predatory impact on micro- and mesozooplankton, a clear positive response of heterotrophic bacteria to the presence of live and dead Aurelia was observed.

Key words: *Aurelia*, vertical distribution, C, N, P contents, microbial plankton, Adriatic Sea

POPOLAZIONE DI AURELIA SP. 5 (SCYPHOZOA) NEL LAGO DI MLJET (ADRIATICO MERIDIONALE): INTERAZIONI TROFICHE E LEGAME CON LA RETE ALIMENTARE MICROBICA

SINTESI

Gli autori presentano la distribuzione verticale, la composizione chimica e la struttura della popolazione di scifomeduse Aurelia sp. 5, studiata nel lago Mediterraneo eualino sull'isola di Mljet (Veliko jezero, Adriatico meridionale), dove dense aggregazioni sono state osservate nel corso dell'anno. Durante il periodo estivo, la maggioranza degli individui di Aurelia era situata, per gran parte della giornata, nello strato sottostante il termoclino, con temperature fra i 13 e i 19 °C, mentre in ottobre la popolazione si trovava in acque più superficiali. Le meduse migravano verso la superficie all'imbrunire, ma raramente oltrepassavano il termoclino. L'analisi elementare di Aurelia ha rivelato un basso peso secco specifico in contenuti di carbonio, azoto e fosforo, variando rispettivamente fra 0,9–1,7%, 0,2–0,5% e 0,02–0,06%. A prescindere dall'impatto diretto di predazione su micro- e mesozooplankton, è stata registrata una chiara risposta positiva dei batteri eterotrofi alla presenza di esemplari di Aurelia vivi e morti.

Parole chiave: *Aurelia*, distribuzione verticale, contenuti C, N, P, plancton microbico, mare Adriatico

INTRODUCTION

The classical linear planktonic food chain that described transfer of material from dissolved nutrients through phytoplankton to herbivorous and carnivorous mesozooplankton was changed radically by the discovery of the 'microbial loop' more than two decades ago (Azam *et al.*, 1983). At the opposite end of the marine planktonic size-spectrum, more recently we have also modified our understanding of the importance, trophic position and ecosystem role of jellyfish. Traditionally, jellyfish were viewed as a single functional group (Pauly *et al.*, 2009) largely unpalatable to consumers due to high water content, nematocysts and toxins (*e.g.*, Shanks & Graham, 1988), and thus significant for organic matter cycling only as 'top' predators. However, recent discovery of diverse feeding modes (Costello *et al.*, 2008), widespread and frequently massive presence (Purcell *et al.*, 2007), and the fact that even some large marine animals such as sunfish (*Mola mola*) and leatherback turtles (*Dermochelys coriacea*) prey on jellyfish (Houghton *et al.*, 2006), has changed our perception of jellyfish as a dead-end in food webs. Jellyfish were conventionally viewed as voracious predators feeding mainly on mesozooplankton and competing for food with pelagic fish (Purcell & Sturdevant, 2001).

An important factor for the assessment of an organism's trophic position is its biochemical composition, and it is likely that differences in composition will affect their biogeochemical role. Recently, the role of jellyfish in elemental cycling has been reviewed (Pitt *et al.*, 2009) with special attention to the accumulation and release of inorganic and organic carbon, nitrogen and phosphorus. Excretion of dissolved organic matter as a nutrient source for bacterioplankton was also discussed, although it was stressed that very few data were available. A study on the linkage between jellyfish and microbes was carried out in a jellyfish (*Periphylla periphylla*) dominated fjord, where it was found that the layer of maximal jellyfish biomass coincided with elevated total organic carbon, bacterial production and ectoenzymatic activities (Riemann *et al.*, 2006). Another study conducted in this fjord found the microbial community clearly responding to dead jellyfish in different ways; some morphotypes proliferated while others were inhibited by jellyfish tissue (Titelman *et al.*, 2006).

The moon jellyfish *Aurelia* spp. is a cosmopolitan genus but molecular criteria used in recent evolutionary studies indicate that it includes numerous cryptic species (Dawson, 2003). *Aurelia* can form large aggregations, particularly in enclosed seas (the Adriatic, Baltic, Black, Seto Inland, Wadden seas) and in protected coastal waters such as fjords, bays, estuaries and marine lakes where it often attains very high biomass (Lucas, 2001). In many cases *Aurelia* has significant impact on plankton communities, and its structuring effect on mesozooplankton has

been demonstrated in several coastal environments (Olesen, 1995; Omori *et al.*, 1995; Lucas *et al.*, 1997; Schneider & Behrends, 1998; Barz & Hirche, 2005).

Several studies have also linked jellyfish to the microbial loop via direct consumption of ciliates (Stoecker *et al.*, 1987; Båmstedt, 1990; Omori *et al.*, 1995). High clearance rates for nauplii and naked ciliates were found by Malej *et al.* (2007) who pointed to indirect cascading effects of *Aurelia* on the microbial loop in addition to its impact on the entire food web. A more direct connection with bacterioplankton which may use DOC released by *Aurelia aurita* was suggested by Hansson & Norrman (1995).

Our study on the *Aurelia* sp. 5 population and its links to the microbial food web was carried out in a Mediterranean euhaline lake, where dense aggregations have been observed throughout the year (Benović *et al.*, 2000). Genus *Aurelia* is present in the shallow northern Adriatic and in some semi-enclosed bays and lagoons along the eastern and western Adriatic. It has traditionally been termed *A. aurita* although molecular criteria used in recent studies questioned this designation (Schroth *et al.*, 2002; Dawson, 2003); following these authors we use *Aurelia* sp. 5 for the Mljet lake population.

Large (110 L) and small (8 L) mesocosm experiments were used to study the influence of *Aurelia* sp. 5 on microbial biomass and production (Turk *et al.*, 2008) and the response of the native bacterial community to biomass originating from dead *Aurelia* (Tinta *et al.*, submitted). We report here on the vertical position, seasonal size structure, and elemental composition (C, N, P) of *Aurelia* and discuss these data in relation to microbial plankton.

MATERIAL AND METHODS

Our study was conducted in a euhaline marine 'lake' located on the north-western side of Mljet, an offshore south Adriatic island. Veliko jezero (Big Lake – BL, see Fig. 1 in Graham *et al.*, 2009) is a submerged karstic depression that was flooded during Holocene sea-level rise (Wunsam *et al.*, 1999). Exchange between this small lake (surface area about 1.45 km²) and the open Adriatic is through a 1 km long and 10 m wide channel that was artificially deepened to about 2.8 m (Ridžanović & Šimunović, 1995). Weak tides (< 25 cm tidal range) restrict water exchange with the open sea through the channel. The lake bathymetry has two main depressions (depths > 40 m) separated by a sill (depth < 15 m), which affect the environmental and biological characteristics of the lake. During summer, a strong thermocline separates the 12–20 m deep upper layer from deeper waters where temperature is rather stable throughout the year (9–12 °C). Maximal surface temperatures may reach 26–28 °C. Small salinity differences between the surface layer (36.3–38.6 psu) and deeper layer (37.5–38.6 psu) also exist (Fig. 1).

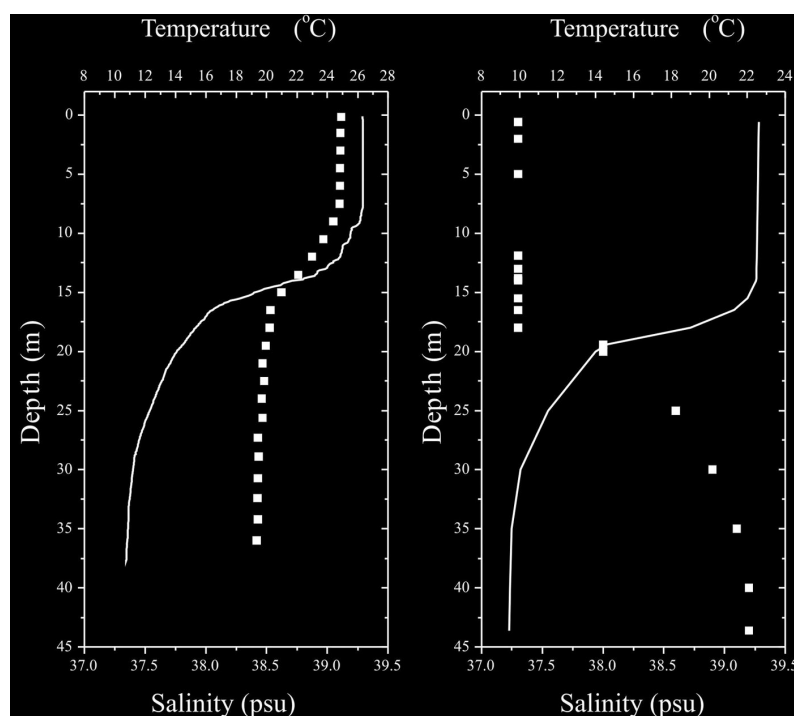


Fig. 1: Temperature (solid line) and salinity (solid square) profiles in July 2003 (left) and October 2006 (right).
Sl. 1: Temperatura (polna črta) in slanost (polni kvadrati) julija 2003 (levo) in oktobra 2006 (desno).

The water column characteristics and *Aurelia* vertical distribution were studied in the two deepest areas of BL (Fig. 1, Graham *et al.*, 2009). A CTD fine-scale probe (Microstructure Profiler MSS90, Sea & Sun Technology GmbH) was used to determine temperature and salinity, and vertical distribution of *Aurelia* was assessed using a Sony DCR-VX200E video camera in an Ikellite underwater housing.

Aurelia were collected either with a zooplankton net (WP2, 200 µm mesh) or manually by divers during following periods: 4–18 July 2003, 16–23 May 2004, 20–21 July 2005, 6–10 March 2006, 3–6 October 2006, 6–16 May 2008, 14–23 May 2009. For bell diameter measurements, medusae were spread flat on a glass plate and the diameter was recorded to the nearest 1 mm. *Aurelia* were stored individually in bags for elemental analysis and kept deep-frozen (–30 °C). Samples were freeze-dried and chemically analysed using a CHN elemental analyzer (CarloErba). Phosphorous was estimated after digestion of samples with K₂S₂O₈ in an autoclave and subsequent colorimetric detection of phosphate produced (Grasshoff *et al.*, 1983).

The concentration of Chlorophyll *a* in the water samples was determined using the reverse-phase HPLC (High Performance Liquid Chromatography) method (Mantoura & Llewellyn 1983; Barlow *et al.*, 1993) and by absorbance at 440 nm using a UV/Vis spectrophotometric detector (Spectra Physics, Model UV2000).

Bacterial abundance and production were deter-

mined using standard procedures of staining formalin-fixed samples with DAPI (Porter & Feig, 1980) and bacterial protein synthesis using ³H-Leucine (Smith & Azam, 1992); methodology used is described in detail in Turk *et al.* (2008).

RESULTS AND DISCUSSION

Vertical distribution

Vertical distribution of *Aurelia* was followed over several diel cycles in the deepest parts of the lake (> 40 m). There was a clear difference in vertical position of *Aurelia* population over the diel cycle in October, particularly when compared to months when surface temperatures were > 26 °C (Fig. 2). In summer during the day, most *Aurelia* were below the thermocline in a layer with temperatures of 13–19 °C. They migrated towards the surface at dusk but rarely crossed the thermocline. In October, the population was located shallower during daylight, occupying mostly the thermocline layer with similar temperatures as during summer (see Fig. 1 for temperature and salinity profiles). The water column was still thermally stratified in October although temperature differences between surface and 20 m depth were significantly smaller (about 8 °C) than in July (about 16 °C). At night most medusae were below the thermocline. *Aurelia* were very rarely observed in surface layers (< 5 m; temperatures higher than 20 °C) during any season.

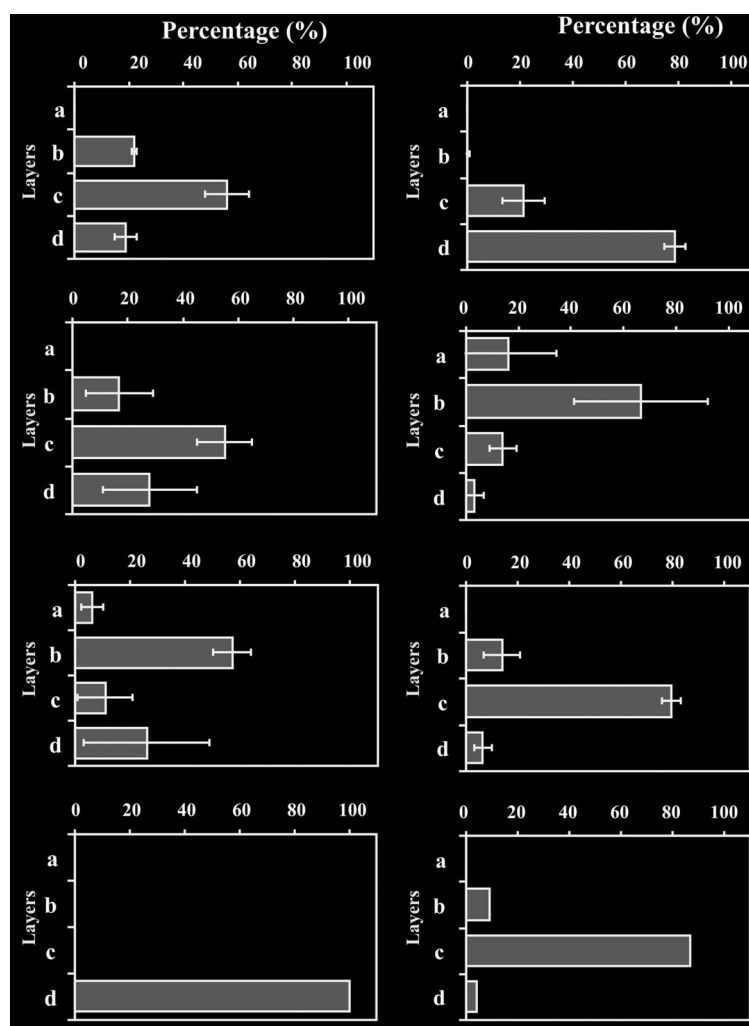


Fig. 2: Vertical position of *Aurelia* population over the diel cycle in July 2003 (left) and October 2006 (right) in different layers: a – above the thermocline layer, b – the thermocline layer, c – below the thermocline layer, d – deep layer (> 25 m). Times of the day (local hour): early morning (04:30–7:30), day (7:30–17:30), dusk (17:30–20:30), night (20:30–04:30).

Sl. 2: Vertikalna razporeditev populacije *Aurelia* v dnevno-nočnem ciklusu julija 2003 (levo) in oktobra 2006 (desno) po slojih: a – sloj nad termoklino, b – termoklinski sloj, c – sloj pod termoklino, d – globoki sloj (> 25 m). Ure (lokalni čas): zgodnje jutro (04:30–7:30), dan (7:30–17:30), večer (17:30–20:30), noč (20:30–04:30).

Short-term (< 60 min) surface swarming was observed on rare occasions during periods of very calm weather during summer and autumn. We did not determine vertical distribution of *Aurelia* population during winter (February–March), but divers that collected jellyfish for bell diameter and elemental analysis reported aggregations between 15 and 5 m.

Population characteristics

Medusae from BL were sampled in all seasons but more frequently during the warmer part of the year. In other temperate marine systems with *Aurelia* popula-

tions, medusae tend to show seasonality with winter-spring recruitment of ephyrae, spring growth, followed by summer accumulation of medusae biomass and eventual disappearance from the water column in autumn (Lucas, 2001). However, *Aurelia* in BL do not show distinct seasonal dynamics. Medusae are present year-round, and from our data we could not see a clear seasonal recruitment and growth (Fig. 2). Presumably, there is an extended recruitment period of new medusae from benthic scyphopolyp in this lake. Bell diameter varied from 2.8 cm in May (2009) to 18.8 cm in July (2006) with the largest average and median diameter in October. However, large year-to-year variability of me-

Tab. 1: Mean size and weight of measured jellyfish (*Aurelia*) during 2003–2009.**Tab. 1: Srednje vrednosti premera klobuka in mokre mase izmerjenih meduz (*Aurelia*) v obdobju 2003–2009.**

	Bell diameter (cm)	Wet weight (g)
Average	8.4	42.3
SD	2.9	46.7
Median	8.2	25.0
Min	2.8	10.0
Max	18.5	380.0
N	379	379

dusae size in the same period was also found (Fig. 3) and May samples (collected in three years: 2004, 2008, and 2009) clearly illustrate this divergence. Mean wet weight (Tab. 1) of *Aurelia* individuals was rather low and showed a seasonal pattern that matched bell diameter, with slightly higher values in July compared to March and May and with maximum weight in October.

Elemental analysis of *Aurelia* reveals low dry weight specific carbon and nitrogen content (Fig. 4) ranging from 0.9 to 1.7% and 0.2 and 0.5% for carbon and nitrogen, respectively, and rather low C/N atomic ratios

(3.9–4.9). Similarly, phosphorus content of *Aurelia* was low with an overall average of 0.04% of dry weight. These contents are comparable to other gelatinous plankton but lower than some other Scyphomedusae (Larson, 1986; Malej et al., 1993) as well as *Aurelia* from the northern Adriatic (Malej et al., 2006). Proteins represent the largest organic fraction consistent with low atomic C/N ratio (4.3 ± 0.21). Some seasonal differences were observed with significantly higher organic contents in samples collected in October ($p < 0.01$).

Aurelia-associated organic mass in BL

The average October 2006 values of DW (3% of wet weight), carbon (1.3% of DW), nitrogen (0.3% of DW) and phosphorous (0.04% of DW) contents were applied to abundance estimates of *Aurelia* based on acoustic surveys done during the same period (Alvarez Colombo et al., 2009) to calculate total *Aurelia*-associated mass in the BL (Tab. 2). Taking into account the BL volume, these values translate to average *Aurelia* wet mass of 19.63 g m^{-3} and organic carbon, nitrogen and phosphorus biomass of 7.9 mg C m^{-3} , 1.8 mg N m^{-3} , and 0.2 mg P m^{-3} , respectively. Since *Aurelia* C, N, P contents and mean size were higher in October compared to other months we may consider these estimates as upper biomass levels.

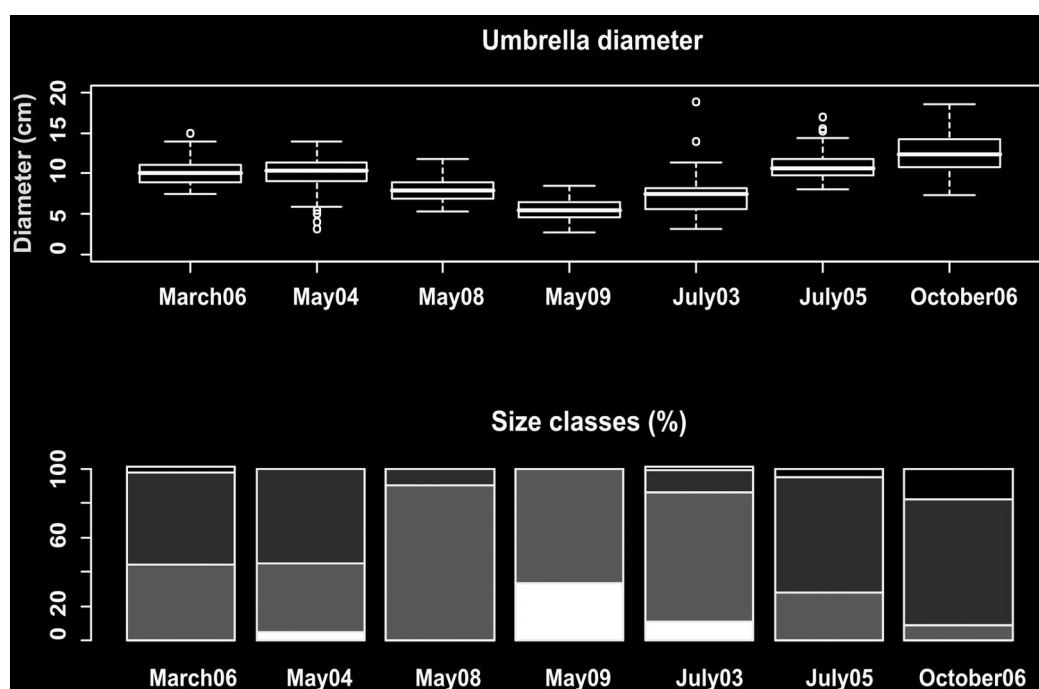


Fig. 3: *Aurelia* median bell diameter (top) and size-frequency distribution (bottom) in different months. Bell diameter (cm): black < 5; dark grey 5–9.9; light grey 10–14.9; white: > 15 cm.

Sl. 3: *Aurelia*: – premer klobuka (mediana, zgoraj) in frekvenčna distribucija (spodaj) v različnih mesecih. Premer klobuka (cm): črno < 5; temno sivo 5–9.9; svetlo sivo 10–14.9; belo: > 15 cm.

Tab. 2: Carbon, nitrogen and phosphorus biomass of *Aurelia* population in the Big Lake (BL) during October 2006 (* from Alvarez Colombo et al., 2009).

Tab. 2: Biomasa populacije *Aurelia* v Velikem jezeru (BL), izražena kot mokra masa, ogljik, dušik in fosfor (* po Alvarez Colombo et al., 2009).

Abundance*		4,238,602
Wet mass	per lake	745,993 kg
	per m ³	19.63 g m ⁻³
C biomass	per lake	291 kg
	per m ³	7.9 mg C m ⁻³
N biomass	per lake	67 kg
	per m ³	1.8 mg N m ⁻³
P biomass	per lake	8.9 kg
	per m ³	0.2 mg P m ⁻³

Top-down control and *Aurelia* as a source of nutrients

Gut content analyses and *in situ* enclosure experiments indicated small copepods, copepodites (*Paracalanus parvus*, *Oithona nana*) and nauplii, followed by naked ciliates, which are the most important prey of *Aurelia*. Other prey items (mollusc larvae, cirripedia nauplii, *Limacina*) were seasonally abundant in guts. Malej et al. (2007) speculated that this top-down control of the food web is responsible for lower zooplankton abundance and reduced number of species in Mljet's Veliko jezero compared to the neighbouring open Adriatic waters.

In addition to the direct predatory impact on micro- and mesozooplankton, a clear response of heterotrophic bacteria (Turk et al., 2008) to the presence of *Aurelia* in mesocosm experiments was also observed as an increase of bacterial biomass (average 1.8 µg C L⁻¹) and production (average 1.8 µg C L⁻¹ d⁻¹). Microbial plankton dynamics in the BL are not well-understood, and few data exist on abundance and production of microorganisms in this system. Most of our analyses were conducted during the warm stratified period when it is expected that abundance and production of autotrophic and heterotrophic microbial plankton are higher than during the cooler periods of the year. The highest chlorophyll *a* concentrations were found in the thermocline layer and were between 233–423 ng L⁻¹ in July 2003 (Fig. 5, right). During the same period, numbers of heterotrophic bacteria varied between 5.0 and 8.9 × 10⁸ cells L⁻¹, with elevated abundance above and below the thermocline layer (Fig. 4, left). In contrast to abundance, bacterial growth tended to be higher at the thermocline layer with an average value of 2.7 µg C L⁻¹ d⁻¹, compared to 2.4 µg C L⁻¹ d⁻¹ and 0.5 µg C L⁻¹ d⁻¹, above and below the

thermocline, respectively (Fig. 4, middle). These results of bacterial abundance and production rates differ only slightly from those found in the more eutrophic Gulf of Trieste and are consistently higher than in the southern Adriatic waters (Tab. 3).

Aurelia could be a substantial source of nutrients for bacteria in the BL where average phytoplankton biomass is nearly an order of magnitude lower (Carić & Jasprica, 1995) than in the Gulf of Trieste (Turk et al., 2007). Applying the weight normalized carbon release rate of 0.012 mg C g⁻¹ wet weight/d (Hanson & Normman, 1995) to data on *Aurelia* in BL during October suggests the whole BL *Aurelia* population releases 8.9 kg C d⁻¹. Applying nitrogen (ammonium) and phosphorus (phosphate) excretion rates by *Aurelia* determined by Shimauchi & Uye (2007) we estimate 2.3 kg N d⁻¹ and 0.26 kg P d⁻¹ was released across the whole lake in October. These values indicate that *Aurelia* released about 3%, 3.4%, and 2.9% of its carbon, nitrogen and phosphorus biomass daily. These values do appear comparatively

Tab. 3: Comparison of data for bacterial abundance and bacterial carbon production for different areas in the Adriatic Sea.

Tab. 3: Primerjava bakterijske abundance in produkcije v različnih območjih Jadranskega morja.

Area	Abundance (× 10 ⁸ cells l ⁻¹)	Bacterial carbon production (µg C l ⁻¹ d ⁻¹)	Reference
Mljet, Veliko jezero	4.7–8.9	0.68–4.3	This work
Southern Adriatic	1.31–1.61	0.24–4.80	Corinaldesi et al., 2003
Middle Adriatic Sea	8.8±0.06	17.19±1.99	Šolić & Krstulović, 1994
Middle Adriatic Sea	2.0–10		Šestanović et al., 2004
Northern Adriatic	1.0–60		Fuks et al., 2005
Gulf of Trieste	4.4–17	0.5–16.0	Turk and Hagström, 1994; Turk et al., 2001
Gulf of Trieste	0.06–18.5	9.6–55.2	Pugnetti et al., 2005

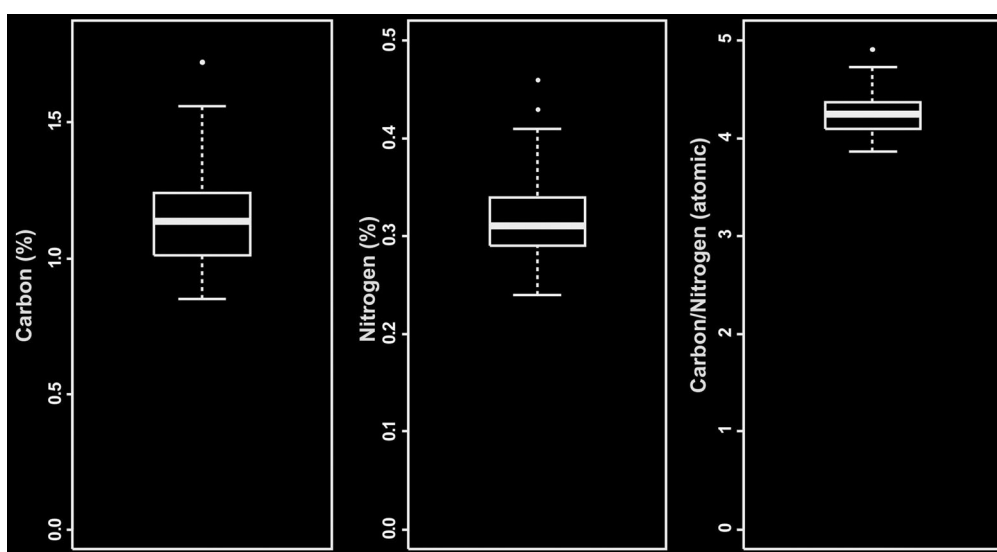


Fig. 4: Aurelia carbon and nitrogen contents (as % of dry weight) and atomic C/N ratio.

Sl. 4: Aurelia – vsebnost ogljika in dušika (% suhe mase) in atomsko C/N razmerje.

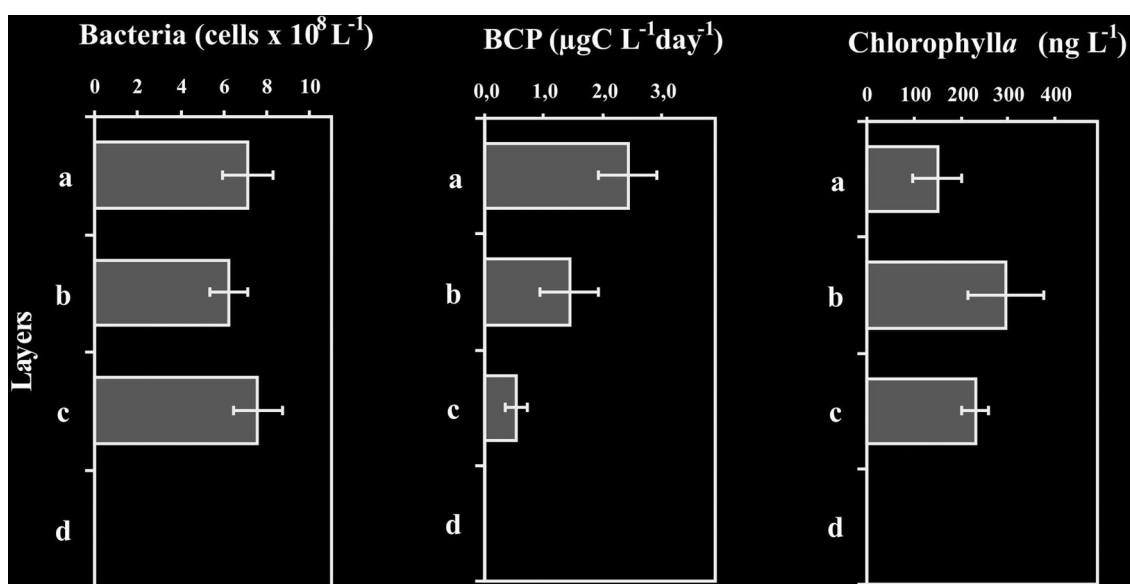


Fig 5: Vertical distribution of an average bacterial number (left), bacterial carbon production (middle) and chlorophyll a concentrations (left) in July 2003 in different layers: a – above the thermocline layer, b – the thermocline layer, c – below the thermocline layer, d – deep layer (> 25 m).

Sl. 5: Vertikalna razporeditev povprečnega števila bakterij (levo), bakterijske produkcije (sredina) in koncentracij klorofila a (levo) v juliju 2003 v različnih slojih: a – sloj nad termoklino, b – termoklinski sloj, c – sloj pod termoklino, d – globoki sloj (> 25 m).

high and should be considered as very preliminary since we do not have direct excretion measurements. Moreover, Shimauchi & Uye (2007) carried out excretion experiments at temperatures that were higher than favoured by Mljet *Aurelia* population, as inferred from their prevailing vertical distribution.

Dead *Aurelia* are likely to be an important nutrient source for bacteria in the lake. Enclosure experiments investigating degradation rates of *Aurelia* homogenates from the Mljet Lake show a more rapid response of the lake's bacterial community when compared to the Gulf of Trieste (Tinta *et al.*, submitted). In addition to different measured response times, changes in community com-

position also diverged in the two ecosystems. The addition of jellyfish tissue did not trigger large changes in the Mljet Lake bacterial community; however, it resulted in changes in the Gulf of Trieste communities, as determined by genetic fingerprinting. In conclusion, we found out that the lake's bacterial community is well adapted to utilize this type of substrate. *Aurelia* provide significant nutrient sources for bacterioplankton in addition to direct predatory pressure on meso- and micro-zooplankton and indirect cascading effect on microbial plankton.

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POPULACIJA VRSTE *AURELIA* SP. 5 (SCYPHOZOA) V MLJETSKEM JEZERU (JUŽNO JADRANSKO MORJE): TROFIČNE INTERAKCIJE IN POVEZAVA Z MIKROBNIM PREHRAMBENIM SPLETOM

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POVZETEK

Študija vertikalne distribucije, strukture in kemijske sestave populacije skifomeduz *Aurelia* sp. 5 je bila narejena v sredozemskem slanem jezeru na otoku Mljetu (Veliko jezero, južni Jadran), kjer se skozi vse leto pojavljajo goste združbe teh organizmov. Večina meduz se je poleti skozi večji del dneva nahajala v sloju pod termoklino 13–19 °C, medtem ko je bila populacija oktobra v plitvejši vodi. Meduze so se proti gladini pomikale zvečer, a zelo redko prečkale termoklino. Elementna analiza meduz je v suhi masi pokazala nizko specifično vsebnost ogljika, dušika in fosforja od 0,9–1,7%, 0,2–0,5% in 0,02–0,06% za ogljik, dušik in fosfor. Poleg neposrednega plenilskega vpliva na mikro- in mezozooplankton so raziskovalci zabeležili tudi jasen pozitiven odziv heterotrofnih bakterij na prisotnost živih in mrtvih *Aurelia*.

Ključne besede: *Aurelia*, vertikalna distribucija, vsebnost ogljika (C), dušika (N) in fosforja (P), mikrobni plankton, Jadransko morje.

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EARLY DEVELOPMENTAL SEQUENCE OF AN ANTHOZOAN PARASITE OF THE JELLYFISH *AURELIA* SP. 5 IN AN ISOLATED MARINE LAKE (MLJET, CROATIA)

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ABSTRACT

Gelatinous zooplankton, including planktonic cnidarians, ctenophores and tunicates, share a common population dynamic of boom-bust 'bloom' cycles. Most research tends to emphasize bloom formation, and considerably less attention is paid to factors that ultimately regulate the magnitude, extent and duration of the bloom. Among these are physiological tolerances (i.e., seasonality), food-limitation, predation, and the poorly-understood role of parasitism. We have discovered in the nearly-enclosed marine 'lakes' of Mljet Island (Croatia) an interesting host-parasite association between a quasi-stable year-round population of the scyphomedusa *Aurelia* sp. 5 and the early and larval parasitic stages of an anthozoan. In this paper we describe the rapid (~72 hr) sequence of early development in this anthozoan. While the species-level identity of the anthozoan remains uncertain, we still provide the first description of the entire sequence of the early developmental stages for parasitic anthozoans. Our ultimate aim is to understand the basic ecology of this host-parasite relationship to further determine whether parasitism is an important factor in *Aurelia* sp. 5 population regulation in the Mljet lakes ecosystem.

Key words: scyphomedusae, population regulation, *Peachia*, *Halcampa*, *Edwardsiella*

SEQUENZA INIZIALE DI SVILUPPO DI UN ANTOZOO PARASSITA DELLA MEDUSA *AURELIA* SP. 5 IN UN LAGO MARINO ISOLATO (MLJET, CROAZIA)

SINTESI

Lo zooplankton gelatinoso (inclusi cnidari, ctenofori e tunicati planctonici) condivide una comune dinamica ciclica con aumenti e ricadute della popolazione. Molte ricerche tendono ad enfatizzare la formazione delle cosiddette fioriture, e quindi meno attenzione viene prestata ai fattori che in definitiva regolano la magnitudine, l'estensione e la durata della fioritura. Fra tali fattori spiccano tolleranze fisiologiche (stagionalità), limitazione alimentare, predazione ed il mal compreso ruolo del parassitismo. Gli autori hanno scoperto nei semi-chiusi "laghi" marini dell'isola di Mljet (Croazia) un'interessante associazione ospite-parassita, fra una quasi stabile popolazione di scifomedusa *Aurelia* sp. 5, presente tutto l'anno, ed una fase di sviluppo iniziale ed una fase larvale parassitica di un antozoo. Nell'articolo viene descritta la rapida sequenza (~72 ore) della fase iniziale di sviluppo di tale antozoo. Benché l'identificazione a livello di specie dell'antozoo resti ancora incerta, viene comunque fornita una prima descrizione dell'intera sequenza delle fasi iniziali di sviluppo di antozoi parassiti. Lo scopo finale della ricerca è quello di capire l'ecologia di base della relazione ospite-parassita, al fine di accertare se il parassitismo sia effettivamente un fattore importante nella regolazione della popolazione di *Aurelia* sp. 5 nell'ecosistema dei laghi di Mljet.

Parole chiave: scyphomedusae, regolazione della popolazione, *Peachia*, *Halcampa*, *Edwardsiella*

INTRODUCTION

Macro-parasitism is one of the greatest, if not the greatest, sources of morbidity in multi-cellular eukaryotic populations (Anderson & May, 1978). Our general knowledge of parasitism in the sea is far more limited in comparison to terrestrial systems, but parasitism nevertheless may be equally important in regulating host populations of marine species. Thus it would be truly beneficial to understand the nature of parasitism as a source of morbidity leading to reduced fecundity or survival in populations of nuisance blooms of gelatinous zooplankton such as medusae.

The association between gelatinous zooplankton (hydromedusae, scyphomedusae, ctenophores, and pelagic tunicates) and ectoparasitic crustaceans such as amphipods has been studied in detail (Laval, 1980; Buecher *et al.*, 2001; Gasca & Haddock, 2004). The ecto- and endoparasitic association between gelatinous zooplankton and anthozoan sea anemones has been reported numerous times in the literature (Müller, 1860; Haddon, 1886-87; McIntosh, 1887; Haddon, 1888; Badham, 1917; Blackburn, 1948; Nyholm, 1949; Spaulding, 1972; 1974; Crowell, 1976; McDermott *et al.*, 1982; Bumann & Puls, 1996), but ecological studies are lacking (Arai, 1997). There is the additional uncertainty regarding the taxonomy of parasitic anthozoans because the phenomenon usually involves the anthozoan larval and juvenile stages, which remain poorly described, highly variable or entirely unknown (Spaulding, 1972; 1974; Shick, 1991; Fautin, 2002). Very few successful attempts have been made to culture parasitic larvae to recognizable adults (Spaulding, 1972; 1974; Crowell, 1976).

As shown in Table 1, the larval forms of the genera *Peachia* spp. and *Edwardsiella* spp. are the most commonly reported parasites of hydromedusae, scyphomedusae and ctenophores (Müller, 1860; Haddon, 1886-87; McIntosh, 1887; Badham, 1917; Blackburn, 1948; Spaulding, 1972; Crowell, 1976; McDermott *et al.*, 1982; Bu-

mann & Puls, 1996). *Edwardsia lineata* reported by Bumann & Puls (1996) is synonymous with *Edwardsiella lineata* (Verrill in Baird, 1873). *Halcampa chrysanthellum* reported by Haddon (1886-87) is recognized as *H. duodecimcirrata* (M.Sars, 1851), but the genus *Halcampa* spp. has been rarely mentioned as a parasite on jellyfish. *Philomedusa vogtii* cited by Müller (1860) is likely a misidentification by that author as the species has not been observed since.

As part of the large multinational "Meduza" research program investigating the ecology of gelatinous zooplankton in the southern Adriatic Sea region, we initiated an observational study on the reproductive patterns of the resident scyphomedusa, *Aurelia* sp. 5 (Dawson & Jacobs, 2001). This species, described ecologically elsewhere (Benović *et al.*, 2000; Malej *et al.*, 2007; Alvarez Colombo *et al.*, 2009; Graham *et al.*, 2009) is the dominant macroplanktonic organism in the semi-enclosed 'lakes' of northern Mljet Island (refer to Graham *et al.*, 2009, for a detailed description). This population of *Aurelia* sp. has likely been isolated for several thousand years in the small marine lakes ecosystem of Mljet Island and recent investigations by us (Graham *et al.*, 2009) and others (Malej *et al.*, 2007) point to a quasi-stable year-round population of medusae that may be regulated largely by a combination of bottom-up trophic processes and reduced productivity induced by parasitism (Graham *et al.*, 2009; L. Chiaverano & W. Graham, *unpubl. data*).

During initial field studies in summer 2002, we observed very heavy infections (~50%) of *Aurelia* sp. 5 by a presumed, yet unidentified, anthozoan species. Information regarding identification, developmental patterns and ecological significance of larval anthozoan infections of medusae, in general, is poor, so we have attempted to shed light on this association by describing the early developmental stages of the anthozoan likely responsible for at least a portion of *Aurelia* sp. 5 population regulation in this ecosystem.

Tab. 1: Compilation of anthozoan species described as parasites of specific gelatinous zooplankton.

Tab.1: Seznam koralnjaških vrst, opisanih v vlogi parazitov specifičnega želatinoznega zooplanktona.

Host	Anthozoan	Reference
<i>Olindias</i> sp., <i>Chrysaora</i> sp.	<i>Philomedusa vogtii</i> Müller, 1860	Müller, 1860
Leptomedusae	<i>Halcampa duodecimcirrata</i> (M. Sars, 1851) (reported as <i>Halcampa chrysanthellum</i>)	Haddon, 1886-87
<i>Thaumantias</i> sp.	<i>Peachia</i> sp.	McIntosh, 1887
<i>Catostylus mosaicus</i> (Quoy and Gaimard, 1824) (reported as <i>Crambessa mosaicus</i>)	<i>Peachia hilli</i> Wilsmore, 1911	Badham, 1917
<i>Cyanea capillata</i> (L.) var. <i>marginata</i> von Lendenfeld, 1844	<i>Peachia clava</i> (Quoy and Gaimard, 1833)	Blackburn, 1948
<i>Phialidium gregarium</i> (A. Agassiz, 1862)	<i>Peachia quinquecapitata</i> McMurrich, 1913	Spaulding, 1972
<i>Mnemiopsis leidyi</i> (A. Agassiz, 1965)	<i>Edwardsiella lineata</i> (Verrill in Baird, 1873)	Crowell, 1976
<i>Cyanea capillata</i> (Linnaeus, 1758)	<i>Peachia parasitica</i> (L. Agassiz, 1859)	McDermott <i>et al.</i> , 1982
<i>Mnemiopsis leidyi</i> (A. Agassiz, 1965)	<i>Edwardsiella lineata</i> (Verrill in Baird, 1873) (reported as <i>Edwardsia lineata</i>)	Bumann & Puls, 1996

MATERIALS AND METHODS

Sampling and observations

All specimens of *Aurelia* sp. 5 medusae were collected in Veliko Jezero by SCUBA divers during July 2003 and May 2004. No more than three medusae, captured by gentle handling, were placed in a given plastic bag and quickly transported to the laboratory usually within 30 min. A total of 15 medusae were examined each year. Individual medusae were measured, photographed and then manipulated with clean glass pipettes to detach parasites from the subumbrellar surfaces and transfer them to multi-chambered petri dishes (chamber volume 15 ml). Each chamber was filled with 'lake' water filtered at 30 µm from the medusa collection sites. No more than five larvae were placed in a chamber. With the exception of observation points, larvae were maintained at 18°C in the dark.

Microscopic observations and digital photographs with scale reference were made twice each day, usually early morning and late afternoon. During the observation period, handling was minimal and limited to observations and photography only. No feeding occurred, though development clearly proceeded. There was no need to provide a substrate or to make additional water changes.

RESULTS

Parasite developmental progression and distribution within *Aurelia* sp. 5 are qualitatively linked. Moreover, presence of infection in *Aurelia* sp. 5 (Fig. 1) is con-

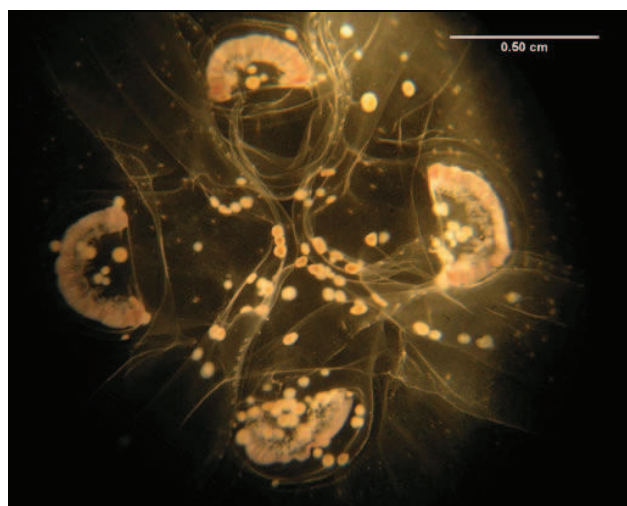


Fig. 1: Gastric cavity of *Aurelia* sp. 5 infected by the anthozoan larvae in Veliko Jezero (Mljet, Croatia).

Sl. 1: Prebavna votlina primerka vrste *Aurelia* sp. 5, okužena z ličinkami koralnjaka v Velikem jezeru (Mljet, Hrvaška).

spicuous as the large (500–600µm) and orange anthozoan zygotes and blastulae are about three times the size of white *Aurelia* sp. 5 ova and developing planulae (~180µm). Earliest parasite developmental stages found only in the gastric pouches of *Aurelia* sp. 5 are zygotes (recently fertilized and showing no evidence of mitotic divisions; Fig. 2a). The development from zygote (assumed to be time 0 hr) to larva was complete in about 72 hr after the beginning of the observation; a synopsis of the timing of each phase is shown in Table 2. The zygote is surrounded by a thin, transparent gelatinous membrane and has a granulated cytoplasm (Fig. 2a). Cleavage was visible after about 12 hr of initial observation of this earliest stage (i.e., not after fertilization; Fig. 2b–c) and leading to the development of the blastula within 18 h (not shown). Gastrulation occurred around 32–36 hr through invagination (Fig. 2d). The transition from gastrula to larva is complete in about 24–36 hr. Larvae (72 h after the beginning of observations; Fig. 2e–f) migrated from the gastrovascular cavity of the medusae to colonize the sub-umbrella, ultimately burrowing either into the epithelial layer or into the radial canals. No larvae older than represented in Figure 2f were observed in any medusa collected.

Tab. 2: Timing of the early developmental stages of the anthozoan parasite on *Aurelia* sp. 5 in Mljet 'lakes' (Croatia).

Tab. 2: Časovni razpored zgodnjih razvojnih faz koralnjaškega parazita na vrsti *Aurelia* sp. 5 v Mljetskih 'jezerih' (Hrvaška).

Developmental stage	Time (hr)
Zygote	0
Cleavage	12
Blastula	18
Gastrula	32–36
Larva	72

DISCUSSION

Our observations on the early developmental sequence of this anthozoan parasite shed light on the ecological processes surrounding this interesting host-parasite relationship. That most of the earlier developmental stages (i.e., fertilized eggs, developing zygotes and blastulas) are located in the medusa gastric cavities indicates that infection occurs shortly after egg fertilization. It also suggests that infection occurs via feeding processes by the *Aurelia*. In other words, recently fertilized anthozoan eggs or individual gametes are broadcast into the water column where medusae subsequently ingest them. This was previously theorized as the mode of infection of the hydromedusa *Phialidium gregarium* by the parasitic anthozoan *Peachia quinquecapitata* (Spaulding, 1972). By presumably avoiding digestion within the gastric pou-

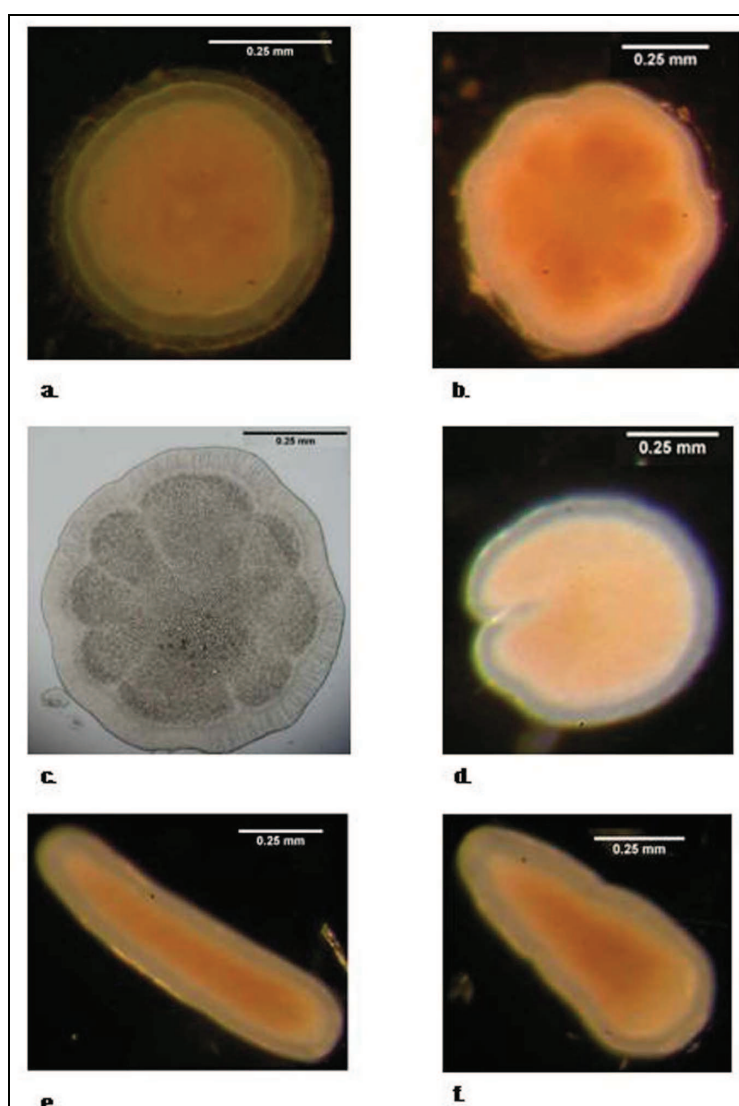


Fig. 2: Developmental stages of the anthozoan parasitizing *Aurelia* sp. 5 in Mljet 'lakes' (Croatia): a = fertilized egg; b, c = cleavage; d = gastrula; e = non contracted larva; f = contracted larva. Scale bars indicate size changes.

Sl. 2: Razvojne faze koralnjaka, ki parazitira vrsto *Aurelia* sp. 5 v Mljetskih 'jezerih' (Hrvaška): a = oplojeno jajčece; b, c = cepitev; d = gastrula; e = neskrčena ličinka; f = skrčena ličinka. Merilo prikazuje spremembe v velikosti.

ches, development proceeds through gastrulation and larval development with most of the later larval stages located in the radial canals of *Aurelia* sp. 5. We can only assume that recruitment of the larval stages back to the still-undescribed adult population occurs after the later-staged larvae emerge from the medusa. Over the course of dozens of dives in all seasons, we have never observed parasites further developed than shown in Figure 2f.

This is the first description of the entire sequence of the early developmental stages of a parasitic anthozoan and, to our knowledge, just the second for all anthozoans since the work of Nyholm (1949). Cnidarians, in general, manifest high developmental variability (Shick, 1991; Fautin, 2002), and developmental stages described by

Nyholm (1949) for *Halcompa duodecimcirrata* (M. Sars, 1851) and by Spaulding (1972, 1974) for *Peachia quinquecapitata* McMurrich (1913) were particularly useful in our attempt to identify basic characteristics of parasitic actiniarian larvae. It is, however, unfortunate that identification below the family level is impossible due to lack of taxonomic information in the recent literature. Moreover, our limited time of about two weeks at the remote field location prohibited the rearing of these larval stages to an identifiable adult stage.

This list of potential candidate genera is limited to *Peachia*, *Halcompa*, and *Edwardsiella*, with the two former genera of most interest as they are widely described as "medusophilous" (Tab. 1). Since we never ob-

served the spiny macrovilli described by Spaulding (1972, 1974) for the eggs of *Peachia quinquecapitata*, we quickly ruled out *Peachia*. A higher level of similarity was instead found with the developmental stages described by Nyholm (1949) for *Halcompa duodecimcirrata*, even though this description was made on free-living developmental stages. One significant structural difference between our parasitic larvae and that of Nyholm's (1949) description is the presence of a thick jelly coat surrounding all the developmental stages.

Recently, however, a molecular genetic analysis on the developing parasites suggested a 16S rRNA region most closely, but not exactly, matching *Edwardsiella* sp. (L. Chiaverano & K. Bayha, *unpubl. data*). Both *Halcompa* sp. and *Peachia* sp. were included in the GenBank reference library, so we are reasonably confident that the Mljet *Aurelia* sp. 5 parasite is neither of these species. Placement within the Edwardsiidae would be an interesting finding as the only ecological descriptions of parasitism are with ctenophores (Crowell, 1976; Bumann & Puls, 1996) and not with cnidarian medusae. Moreover, parasitism has only been reported for post-larval stages of *Edwardsiella* sp., but never for the larval stages (Daly, 2002b; Reitzel *et al.*, 2006). Recent systematic revision of Edwardsiidae (Daly, 2002a) reveals a clustering of all the "medusophilous" genera within the Order Actiniaria, Suborder Nyantheae, Tribe Athenaria.

As a further complication, *Edwardsiella*, *Halcompa* or *Peachia* have not been reported in the checklist of the Anthozoan of Mljet fauna (Kružić, 2002). Rather, the only Athenarian species found close to Veliko Jezero was *Halcompoides purpurea* (Studer, 1879) from outside the lakes (Kružić, 2002). Molecular evidence, however, does not support identification as *Halcompoides* (L. Chiaverano & K. Bayha, *unpubl. data*), and we believe the adult stages simply have not been found due to the lack of effort to survey these small, cryptic anemones in the

Mljet lakes. Including the three described parasite genera mentioned above, there are 48 genera in 10 families, and it may well be that parasitic associations are taxonomically far more common than we previously believed. The accurate identification of the Mljet *Aurelia* sp. 5 parasite may remain unknown until reference DNA is collected and made accessible for comparison with our samples.

We continue to seek a better understanding of the ecology of this parasitic relationship in the Mljet 'lakes'. Parasitism has been documented over repeated trips to the Mljet 'lakes' over 5 years and during three seasons (spring, summer and winter), thus the association appears to be fixed in this system. While the anthozoan parasitism itself is not novel, the magnitude of infection across the *Aurelia* sp. 5 population (as much as 50% of the medusae), extent of infection with individual medusae (see Fig. 1 as an example) and persistence over time, give us a tantalizing picture of jellyfish population regulation by parasites rather than by food-limitation or macropredation. Therefore, we continue to push for a complete understanding of this particular host-parasite relationship with the hope that it will ultimately reveal underlying ecology applicable to jellyfish population dynamics well beyond the boundaries of this remote and isolated marine lake ecosystem.

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ZGODNJA RAZVOJNA SEKVENCA KORALNJAŠKEGA PARAZITA NA MEDUZI VRSTE AURELIA SP. 5 V IZOLIRANEM MORSKEM JEZERU (MLJET, HRVAŠKA)

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POVZETEK

Za populacije želatinoznega zooplanktona, vključno s planktonskimi ožigalkarji, rebračami in plaščarji, je značilna ciklična dinamika izbruhov in upadanj masovnega pojavljanja. Večina raziskav se osredotoča na formiranje tega pojava, precej manj pozornosti pa se namenja dejavnikom, ki regulirajo obseg in trajanje masovnega pojavljanja. Sem vključujemo fiziološke tolerance (npr. sezonskost), omejeno količino hrane, predacijo in slabo razumljeno vlogo parazitizma. V skoraj zaprtih morskih 'jezerih' na otoku Mljetu (Hrvaška) smo odkrili zanimivo razmerje gostitelj-parazit, in sicer med kvazistabilno, skozi vse leto prisotno populacijo klobučnjakov *Aurelia* sp. 5 ter koralnjakov v zgodnji razvojni fazi in parazitski fazi ličinke. V pričujočem članku je opisana hitra (~72 ur) sekvenca zgodnjega razvoja tega koralnjaka. Čeprav še vedno ni popolnoma jasna identiteta koralnjaka na ravni vrste, je tu

prvič opisana celotna sekvenca zgodnje razvojne faze parazitskih koralnjakov. Naš poglavitni cilj je razumeti osnovno ekologijo tega razmerja gostitelj-parazit ter dalje oceniti, ali je parazitizem pomemben dejavnik regulacije populacije vrste *Aurelia* sp. 5 v ekosistemu Mljetskih jezer.

Ključne besede: skifomeduze, regulacija populacije, *Peachia*, *Halcampa*, *Edwardsiella*

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ACOUSTIC OBSERVATIONS OF JELLYFISH DISTRIBUTION IN MALO LAKE (MLJET IS., CROATIA)

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ABSTRACT

An acoustic survey covering Malo Lake (Mljet Is., Croatia) was performed to obtain a synoptic picture of the distribution of acoustically detectable jellyfish and other biota at 120 kHz. Acoustic records from 24 parallel transects were associated with fish schools and with the scyphomedusa Aurelia sp. for which vertical and horizontal distributions were documented. Echointegration and in situ acoustic target strength measurements were employed to estimate medusae abundance, accounting for approximately 500,000 individuals for Malo Lake.

Key words: Hydroacoustics, medusae, Scyphozoa, *Aurelia*, distribution, abundance

OSSERVAZIONI ACUSTICHE DELLA DISTRIBUZIONE DI MEDUSE NEL LAGO MINORE (ISOLA DI MLJET, CROAZIA)

SINTESI

Gli autori hanno portato a termine un'indagine acustica nel Lago Minore (isola di Mljet, Croazia) allo scopo di ottenere un'immagine sinottica della distribuzione di meduse e altri organismi acusticamente distinguibili a 120 kHz. Le misurazioni acustiche derivanti da 24 transetti paralleli sono state associate a banchi di pesci e alle scifomeduse Aurelia sp., per le quali è stata documentata la distribuzione verticale ed orizzontale. Ecointegrazioni e misurazioni acustiche in situ sono state effettuate al fine di valutare l'abbondanza delle meduse, che si aggira intorno ai 500.000 individui per il Lago Minore.

Parole chiave: idroacustica, meduse, Scyphozoa, *Aurelia*, distribuzione, abbondanza

INTRODUCTION

Recent worldwide increases in jellyfish abundances, blooms and related economical and societal problems (Graham, 2001; Hay, 2006; Lynam *et al.*, 2006; Attrill *et al.*, 2007; Purcell, *et al.*, 2007) have focused attention on finding ways to obtain accurate measures of jellyfish abundance, distribution and temporal variability (Brierley *et al.*, 2005; Alvarez Colombo *et al.*, 2009). Traditional surveys based on plankton net trawls, SCUBA diving and underwater videos provide only semi-quantitative estimates. Consequently, the spatial distribution of medusae is generally not well understood.

Recently, acoustics have been employed with increasing refinement for jellyfish population assessment (Brierley *et al.*, 2005; Lynam *et al.*, 2006; Alvarez Colombo *et al.*, 2009; Han & Uye, 2009), and for detailed individual behaviour studies (Alvarez Colombo *et al.*, 2003; Båmstedt *et al.*, 2003; Klevjer *et al.*, 2009). Acoustics has been used effectively also in a variety of different environments, such as deep sea fjords, small salt lakes, large upwelling systems and turbid coastal lagoons and estuaries (Mianzan *et al.*, 2001; Alvarez Colombo *et al.*, 2003, 2009; Båmstedt *et al.*, 2003; Brierley *et al.*, 2005; Lynam *et al.*, 2006; Han & Uye, 2009; Klevjer *et al.*, 2009).

On the north-western side of the offshore island of Mljet (Croatia, the southern Adriatic Sea), there is a system of small seawater lakes in a submerged karstic valley (Fig. 1). Veliko jezero (BL, Big Lake) is the biggest lake on which descriptions of some biotic components and their distributional patterns have been published (Benović *et al.*, 2000; Malej *et al.*, 2007; Alvarez Colombo *et al.*, 2009). Inland and adjacent to this lake, connected to it by a narrow passage, is another smaller lake, Malo jezero (SL, Small Lake), with a surface area of 0.24 km² and a maximum depth of 34 m. Information about biological components of this small lake is scarce but it is also characterized by the presence of medusa *Aurelia* sp. BL is an oligotrophic coastal lake, and the medusae therein persist in the lake throughout the year (Benović *et al.*, 2000). Although the scyphomedusa *Aurelia* is present in the shallow northern portion of the Adriatic Sea and in other semi-enclosed bays along the Adriatic coast, it is absent in open Adriatic waters offshore of Mljet Island (A. Benović, *unpubl. observ.*). The *Aurelia* sp. population in SL seems to wax and wane over the years, disappearing completely then re-populating the next year, perhaps due to influx of medusae from BL (Benović *et al.*, 2000).

Throughout the Adriatic this species has been called *Aurelia aurita* (Linnaeus, 1758). Recent molecular investigations, however, have questioned the traditionally taxonomic designation (Schroth *et al.*, 2002) and now, provisionally, the species is simply called *Aurelia* sp. 5 (Dawson *et al.*, 2005). In the present study, therefore, it is referred to as *Aurelia*.

During October 2006, a field study was carried out at BL employing a scientific echosounder and video-recorder to determine synoptically the distribution, density and biomass of the *Aurelia* population and other biological scatterers like fish (Alvarez Colombo *et al.*, 2009). The *Aurelia* population consisted of approximately 4,200,000 individuals that were mostly aggregated in and below the thermocline during the day. The acoustic techniques used to characterize *Aurelia* in BL, therefore, were used also in the adjacent SL. The *Aurelia* population in SL has been reported to have distributions and behaviour somewhat different than BL population, with a more regular vertical distribution not associated with the thermocline and with the highest abundances in the deeper layers (17–25 m) at densities of 1 to 10 ind. per 100 m⁻³ (Benović *et al.*, 2000).

This paper presents field information on *Aurelia* in SL. The goals are to quantify the population of *Aurelia*, to describe the horizontal and vertical distribution patterns of its aggregations, and the distribution of other biotic components of the ecosystem.

MATERIALS AND METHODS

On October 6, 2006, a 4 m boat was used in SL to conduct an acoustic survey of the entire lake by dividing the surface into 24 parallel transects 20 m apart, perpendicular to the lake's main axis. Given that the complete area was covered in a period of 2 hours, it may be considered that the distributions of the entire *Aurelia* population and other biological scatterers like fish, were synoptically registered (Fig. 1). Acoustic recordings were obtained by means of a SIMRAD EY500 portable echosounder operating at 120 kHz, with a split-beam transducer. Angle and power sample data were recorded, providing simultaneous 20 log R and 40 log R time-varied-gain (TVG) functions for volume backscattering and target strength analysis, respectively. The echosounder was calibrated after sampling with a tungsten carbide calibration sphere following Foote *et al.* (1987). Post processing of echo-data was done with Echoview v. 4.1 software.

Aurelia acoustic target strength (TS) measurements were obtained *in situ*. The TS measurements were obtained while the boat stayed still at the point selected for the calibration process, following the methodology described in Alvarez Colombo *et al.* (2009). Following the same authors, those echotraces showing similar characteristics and individual acoustic signals as the medusae repeatedly sampled in BL in previous days, were then assigned as *Aurelia*. The abundance of *Aurelia* was estimated by echointegration (Foote *et al.*, 1991) for the water column from 2 m below the surface (beyond the transducer's acoustic near-field) to 1m above the bottom (in order to avoid the contribution of small demersal fish). The echograms were divided into intervals of 10

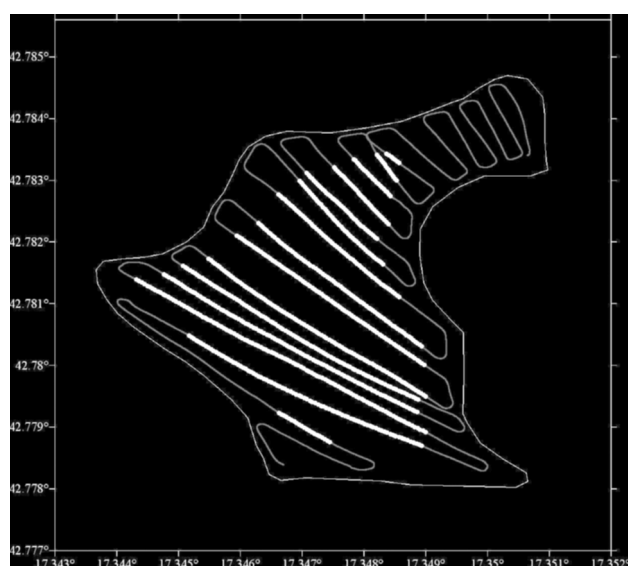


Fig. 1: Map of Malo Lake showing the acoustic track performed (grey line), the sections of the tracks considered for the assessment of *Aurelia* abundance (black lines), and the connection with Veliko Lake (upper right).

Sl. 1: Zemljovid Malega jezera s prikazom opravljenega sonarnega sledenja (siva črta), deli, obravnavani za oceno številčnosti *Aurelia* (črne črte) in povezava z Velikim jezerom (desno zgoraj).

pings, from where the coefficients of acoustic backscattering per unit area s_A ($\text{m}^2 \text{ nmi}^{-2}$) and unit volume S_V (dB, re $1 \text{ m}^2 \text{ m}^{-3}$) were obtained.

The near shore waters were excluded from the analysis of medusae distribution since these sectors contained mostly fish (Fig. 3). The abundance and concentration of individuals C (n m^{-3}) were derived from the echointegration data, using the average backscattering cross-section (σ_{bs}) obtained from *in situ* TS values, as described in Alvarez Colombo *et al.* (2009). An STO Hydrolab Surveyor 3 probe was employed to determine salinity (S), temperature (T), and dissolved oxygen (DO) structure at a station located at the deepest sector of the lake.

RESULTS

Bathymetry

SL has a maximum depth of 32 m in the southern part (Fig. 3) where two noticeable hollows were found. These depressions are 36 and 51 m deep, respectively, confirmed also by divers (O. Pelar, *pers. comm.*). The northern part of SL is shallower and with a more gentle slope.

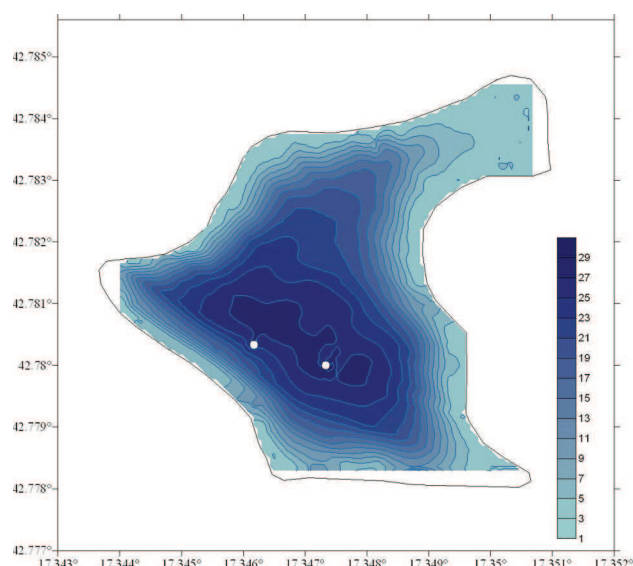


Fig. 2: Bathymetry of Malo Lake, showing the connection with Veliko Lake (upper right). The white circles represent the position of the deep hollows found. Scale in meters.

Sl. 2: Batimetrija Malega jezera z vidno povezavo z Velikim jezerom (desno zgoraj). Bela kroga označujeta položaj najdenih globeli. Legenda je v metrih.

In situ TS measurements

Behaviour of dispersed individual jellyfish in the upper part of the water column resembled that of individuals observed in BL during TS measurements (targets with steady echotrace positions relative to the speed of the drifting boat). Hence, these measurements are considered to reflect the behavioural component (*i.e.* medusa bell contractions/relaxation swimming pulsing and tilt-angle distribution) of the individuals at that moment. Mean medusae TS obtained was -76.69 dB (range = -84.87 to -66.03 dB) (Tab. 1).

Tab. 1: Results of the acoustic and physical parameters employed to estimate the total number of *Aurelia* in Malo Lake (SL).

Tab. 1: Rezultati akustičnih in fizičnih parametrov, uporabljenih za oceno skupnega števila primerkov *Aurelia* v Malem jezeru (SL).

Mean s_A ($\text{m}^2 \text{ nmi}^{-2}$)	3.86
SD	1.66
Mean S_V (dB re $1 \text{ m}^2 \text{ m}^{-3}$)	-83.03
N intervals	880
Area (nmi)	0.03485
σ_{bs} (m^2) (TS = -76.69 dB)	$2.14 \cdot 10^{-8}$
Numerosity (n)	500,480

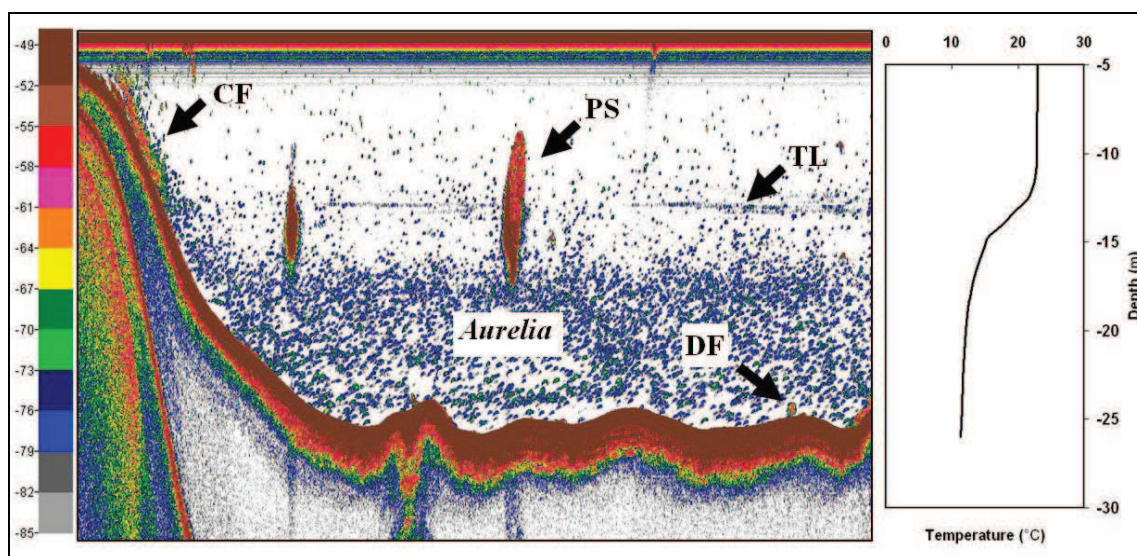


Fig. 3: Vertical distribution of the *Aurelia* population and the different groups recorded in Malo lake: CF = coastal fish; PS = pelagic schools; DF = demersal fish; TL = thermocline layer targets. The temperature vertical profile is presented, showing the thermocline between 12 to 15 meters (right). Scale represents mean volume backscattering strength in dB (left).

Sl. 3: Vertikalna distribucija populacije *Aurelia* in različnih skupin, zabeleženih v Malem jezeru: CF = obalne ribe; PS = pelagične ribje jate; DF = pridnene ribe; TL = skupina v sloju termokline. Prikazan vertikalni temperaturni profil z razvidno termoklino med 12 in 15 metri (desno). Merilo predstavlja povprečni volumen jakosti povratnega sipanja v dB (levo).

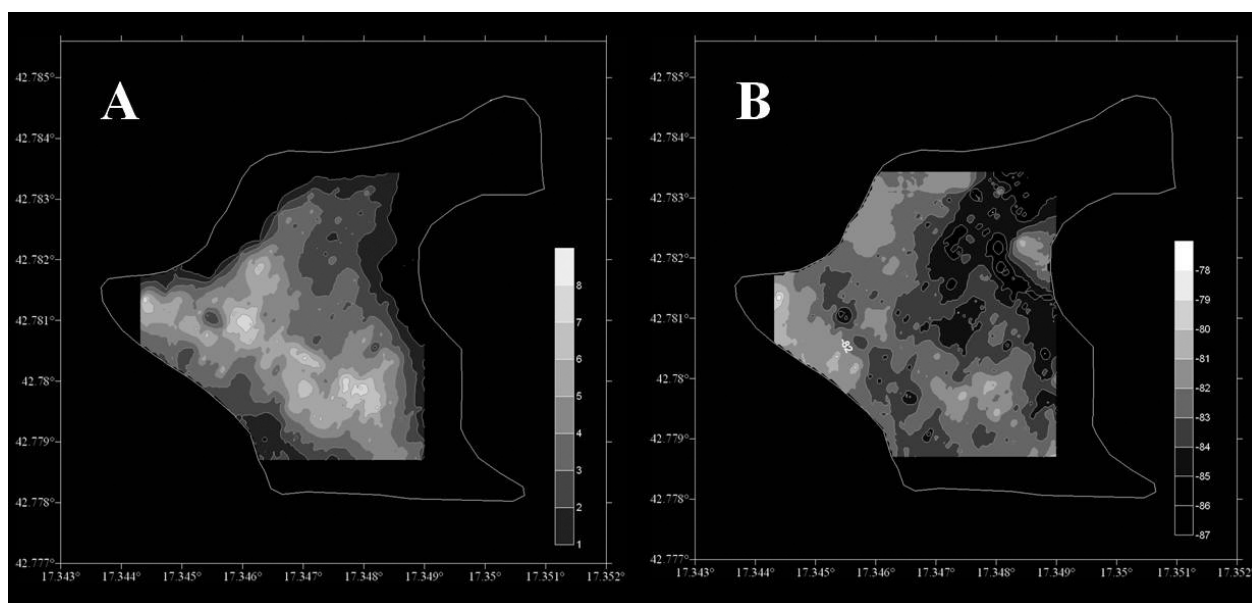


Fig. 4: Interpolation of density data of *Aurelia*, showing patterns of its horizontal distribution. A. Echointegration results in terms of the acoustic coefficient of backscattering strength per unit area (s_A). B. Values of mean volume backscattering strength per unit volume, in decibels (Sv).

Sl. 4: Interpolacija gostote osebkov *Aurelia*, s prikazano horizontalno distribucijo. A. Rezultati ehointegracije kot akustični koeficient jakosti povratnega sipanja na enoto površine (s_A). B. Vrednost povprečnega volumna jakosti povratnega sipanja na enoto prostornine, v decibelih (Sv).

Vertical distribution pattern

A strong thermocline (23 to 14° C) was present at 12 to 15 m. Most medusae were located a couple of meters below the thermocline but some individuals were observed dispersed to the surface (Fig. 3). A thin layer of weak echoes was clearly observed at the thermocline depth, possibly related to aggregations of small zooplankton, marine snow or even sound scattered from the physical interface between two water masses of different densities. Coastal fishes, small demersal fish aggregations and a school of pelagic fish were also observed at different depths along the acoustic track (Fig. 3).

Horizontal distribution patterns

Echo-integrated values of the water column (s_A) showed the largest medusae numbers in the deepest sector of the lake (Fig. 4a). This result was expected considering that the *Aurelia* population was mainly distributed below the thermocline, occupying greater water volumes with an increasing total depth. Also, backscattering values per unit volume showed that more medusae were present near the western margin of the lake (Fig. 4b), possibly related to advection (tidal and/or wind-related circulation). The horizontal distribution of different groups of fish was also recorded. While some schools of pelagic fish were detected in near-shore waters, most of the schools, mainly larger pelagic ones, were recorded in the deeper sector of the lake (Fig. 5).

Acoustic estimation of *Aurelia* abundance

The total number of *Aurelia* inhabiting SL at the moment of the acoustic survey was estimated to 500,480 (Tab. 1). The layer of maximum concentration was recorded between 15 m and the bottom, with a mean density estimated as 0.43 ind. m⁻³.

DISCUSSION

Acoustic techniques were employed to describe the *Aurelia* horizontal and vertical distributions, and estimate its numerical abundance in SL. In doing this, we employed the direct visual evidence and ground-truthing of the echorecordings of the *Aurelia* population in the neighbouring BL. In this sense, the information obtained for this species in SL was similar to the patterns found in the neighbouring BL during the same period (Alvarez Colombo *et al.*, 2009), including congruous vertical distribution of the population during the day. Moreover, behaviour of individual medusae (inferred from echotracés) and the average target strength measured in SL closely matched those of BL.

In addition, the echorecordings allowed us to distinguish medusae from other more actively swimming organisms during the echogram interpretation process. Medusa echoes were separated from the stronger echoes of fish with swimbladders, and from the weaker signals of small zooplankters, as expected from the output of reliable TS models (see Brierley *et al.* 2005).

Aurelia was found mostly below the thermocline, with most of the population concentrated at the deepest sections of the lake, as was also observed in BL. Mean density (0.43 ind. m⁻³) estimated for the maximum concentration layer was close to that calculated for the neighbouring BL (0.52 ind. m⁻³) within the main distribution layer between 15 to 30 m (Alvarez Colombo *et al.*, 2009).

The diurnal vertical distribution of *Aurelia* in SL also resembles that found in BL, with the bulk of the population within and below the thermocline (Malej *et al.*, 2007; Alvarez Colombo *et al.*, 2009). However, in BL the highest densities coincided with the thermocline (Alvarez Colombo *et al.*, 2009) while in SL the medusae layer was located a few meters below.

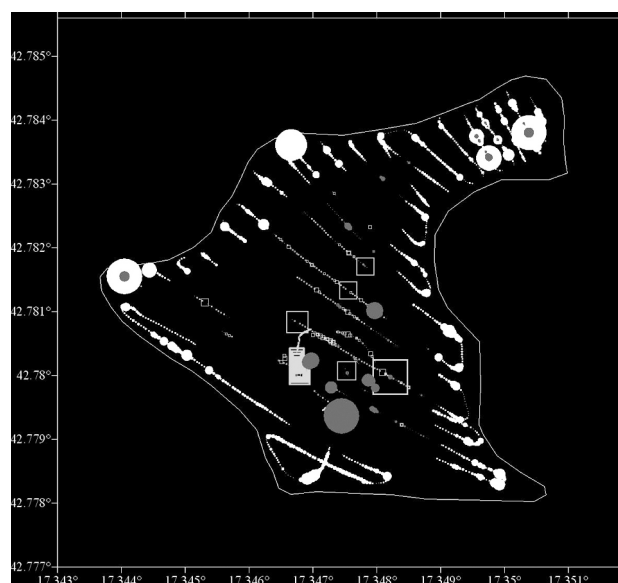


Fig. 5: Horizontal distribution patterns of fish aggregations: black circles = coastal fish; grey circles = pelagic schools; squares = demersal schools. Symbols are proportional to the acoustic coefficient of backscattering strength per unit area (s_A). Note that scales differ between the groups in order to compare distributions.

SL. 5: Vzorci horizontalne distribucije skupin rib: črni krogi = obalne ribe; sivi krogi = pelagične ribje jate; kvadrati = pridnene ribje jate. Velikost krogov je proporcionalna akustičnemu koeficientu jakosti povratnega sipanja na enoto površine (s_A). Merilo se za različne skupine razlikuje zaradi primerjave distribucij.

Based on the absence of ephyrae and because the medusae appear to exhibit a random temporal distribution, it was proposed that the *Aurelia* population in SL originated from BL and was not permanent (Benović *et al.*, 2000). High sedimentation rates observed and the occasional presence of H₂S (Buljan & Špan, 1976; Juračić *et al.*, 1995) in SL was suggested to inhibit planula settlement and the establishment of a permanent local population (Benović *et al.*, 2000). The "stock" of SL coincides with that observed in BL in several features. In both lakes the animals were aggregated mostly in the deepest part of the lake and a similar vertical distribution during daylight was observed, with the same main upper limit of distribution (about 15 m depth), even with a shallower thermocline at SL. The behaviour of individual medusae inferred from echotraces and the average target strength measured (indicative of animal sizes) also closely matched the BL data. In May 2009, an additional survey was performed to check these results using the same boat and gear, but including observations with a ROV. On this occasion, we found no traces of *Aurelia* at all (W. Graham, *pers. comm.*) and the resulting echogram had a completely different signal pattern. All this evidence supports the hypothesis that SL *Aurelia* individuals are advected from BL.

We also obtained information about demersal and pelagic fish distributions and thus our acoustic information provides the basis for future species interactions investigations. In this sense, the acoustic survey of the lake community facilitates the monitoring of the total area synoptically, reduces sampling costs, and dramatically reduces avoidance of the active pelagic organisms such as adult fish and larvae, as expected from the use of sampling devices such as nets (Medwin, 2005).

CONCLUSIONS

The use of bioacoustic techniques allowed us to present for the first time a synoptic picture of the horizontal and vertical distribution of biological components such as different types of fish schools and the scyphomedusa *Aurelia* sp that inhabit Malo Lake. Acoustic signatures allowed us to assign individual echotraces to *Aurelia* sp and a population of 500,480 medusae was estimated for Malo Lake. However, as previously suggested, similarities in medusae distribution between the two connected lakes, and recent observations of the total absence of medusae in Malo Lake in particular years, while still present in Veliko Lake, indicate that the medusae in Malo Lake are not a population unit, but instead advected individuals from Veliko Lake.

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AKUSTIČNA OPAZOVANJA DISTRIBUCIJE MEDUZ V MALEM JEZERU (OTOK MLJET, HRVAŠKA)

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POVZETEK

Informacije o bioloških komponentah Mljetskih jezer so skope. Oligotrofni okolji jezer zaznamuje prisotnost izolirane populacije scifomeduz *Aurelia* sp. v večjem Velikem jezeru potrjeno prisotne skozi vse leto. Za populacijo *Aurelia* sp. v manjšem Malem jezeru, ki pa je z Velikim jezerom povezano, se zdi, da skozi leta raste in se manjša, popolnoma izgine in se naslednje leto obnovi. Z akustičnim vzorčenjem, ki je bilo v Malem jezeru izvedeno tekom dneva 16. oktobra 2006, smo dobili splošno sinoptično sliko distribucije živih organizmov, zaznanih s frekvenco 120 kHz. Ugotovljena je bila vertikalna in horizontalna distribucija organizmov. Pridobljeni podatki o distribuciji različnih ribjih vrst so bili sortirani v obalno, demersalno in pelagično skupino.

Kot je bilo potrjeno že pri pregledu Velikega jezera, akustični zapis ustreza vrsti *Aurelia* sp. Ehointegracijske podatke smo analizirali skupaj z in situ akustičnimi meritvami velikosti ciljne skupine in ocenili, da gre v Malem jezeru za skupaj 500.000 meduz. Splošni dnevni vzorec vertikalne distribucije in velikost ciljne skupine *Aurelia* se ujemata s predhodno pridobljenimi podatki za Veliko jezero. Te ugotovitve, skupaj z odsotnostjo efir in občasno popolno odsotnostjo meduz v Malem jezeru kažejo na možnost, da so primerki *Aurelia* v Malem jezeru pravzaprav z vodnimi tokovi prinešeni posamezni primerki iz Velikega jezera.

Ključne besede: hidroakustika, meduze, Scyphozoa, *Aurelia*, distribucija, številčnost

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